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# A COMPARISON OF STRIP AND QUADRAT ANALYSES OF THE WOODY PLANTS ON A CENTRAL INDIANA RIVER BLUFF

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This report is concerned with the distribution of woody plants on certain river hills in central Indiana. The location is in the vicinity of Blue Bluffs on White river in Morgan county. Most hills, and particularly river hills of a hundred or more feet in height, show certain obvious differences in the woody plants at the top and the bottom. The relative abundance and evenness of distribution of different species, however, is hard to ascertain by ordinary observation, hence various methods of sampling are used to determine more exactly what are the distributional relationships of various species. Strip and sample plot methods of timber estimation have long been in use by the foresters and lumbermen, and out of their methods have grown certain practices of the ecologist. In these studies there has been an effort to compare two methods of statistical analysis of vegetation, (1) sampling by line transects, and (2) sampling by quadrats, or regularly distributed squares.

In the first attempt to determine accurately the distribution of woody species on these river hills, the strip or transect method was used and found to be rapid and easy. The results are interesting and indicative of the conditions of the vegetation, but are not completely satisfactory. The second analysis was made on a basis of quadrats and was found to give more accurate results, but occasioned more work.

If we assume that floristic differences, even of small degree, have ecological significance, then it would seem that a careful statistical analysis of vegetation becomes one of the problems of first importance in an ecological investigation. In a recent discussion of methods in the floristic study of vegetation, Nichols (4) remarks: "If there is any one set of facts which is more susceptible to direct study and exact characterization than any other, it is the floristic composition of the vegetation." As the casual observer may notice, there are flood plain, slope and ridge types of timber, and it is readily apparent that the

moisture and exposure conditions are different at the bottom and the top of a bluff. But, as a special technique is required to ascertain the quantitative differences in soil moisture, soil structure, evaporation, humidity, etc., and to interpret them, so, too, certain technique is necessary quantitatively to determine the presence and distribution of critical or important species in the vegetation. For the student of plant communities, an inadequate description of the floristic composition of the vegetation is as bad as a species description for a taxonomist which would say that a flower was large, or larger, but not how large! Since river hills present abruptly changing habitat differences, they present good plant communities for analysis. A changing habitat means a changing floristic composition of the plant community, and vice versa, so that certain species, at least, we recognize as having considerable ecological significance, while every species must have a certain ecological "equation." In the excellent statement of Nichols, previously quoted, we read: "In general, there can be little question that every species of plant possesses not only a certain more or less definite taxonomic identity, but also a more or less definite ecological individuality. This being true, it follows, as the logical corollary, that any resemblances or differences in the floristic composition of plant communities may be of ecological as well as of taxonomic import."

In the following text the strip transect study will be presented first, and then the analysis by use of quadrats.

## STRIP TRANSECT STUDY

A strip was laid out, starting at the bank of White river (West fork), running directly to the top of Rock Hill, a distance of 650 feet in a southwest direction. The immediate river bank has a slope of 25 degrees, followed by a gentle slope of about 5 degrees for 75 feet, from which flood plain the bluff rises at slopes varying from 15 to 30 degrees from the horizontal, the steepest part being near the summit. At the top of the bluff the transect strip turned 45 degrees to the west and descended into a ravine, a distance of 775 feet. The slope of this portion of the line is generally less steep than that on the side of the river bluff, much of it being from 10 to 20 degrees. The line then continued

west from the ravine upward for a distance of 500 feet to the top of Blue Bluffs, at a slope of from 14 to 28 degrees. The total length of the line is 1,925 feet, while the top of the bluff is 285 feet above the river.

The data were gathered in the following manner: For an entirely separate purpose of hydrogen-ion studies of the soil, soil samples were taken at intervals of twenty-five feet along the line.<sup>1</sup> At each station where a soil sample was taken, a list was made of the trees and shrubs growing within the twenty-five-foot strip. The result was a large number of lists of species representing the succession of plants as they were encountered from the river valley to the top of the river hills, or from the top down, according to the line.

The direction of the line was controlled by compass, and the angle of slope was determined by use of an Abney Hand-Level. In handling these lists of species, it was decided to divide the lists according to altitudinal zones. This was accomplished by plotting on paper the length and angle of slope of the various segments of the line. On this contour of the hills studied were located the positions of the various soil sample stations and the lists of species accompanying them. Five zones were selected arbitrarily, which represent the five columns in Table I. From the river up they are each fifty feet in altitude, except the hilltop zone, which is slightly over. By thus dividing the strip into horizontal zones, it was possible to determine which stations occurred in each zone and, consequently, which species occurred in each zone. The results are presented in Table I.

The percentages given in Table I are not based on the total number of stations (and lists of species) along the whole line, but on the number of such stations occurring in the strip within each altitudinal zone above the river. Although the stations are evenly spaced in the line, the regions of the slopes which are more gradual will have more stations within the fifty-foot rise than those regions which are steeper. Thus we find 10 stations in the hilltop zone, and 13, 18, 20 and 16 stations consecutively in the zones down to the one immediately above the river level. The percentage occurrence of a species within a zone depends then upon the number of times it occurred in the separate

<sup>1</sup>See the following paper, page 172.

TABLE I  
DISTRIBUTION AND FREQUENCY OF SPECIES FROM  
RIVER-BLUFF TRANSECTS

SPECIES	Percentage Occurrence Based on Altitude Classes (Height in feet above the river)				
	200-285	150-200	100-150	50-100	0-50
<i>Gaylussacia baccata</i> .....	10	---	---	---	---
<i>Populus grandidentata</i> .....	50	8	---	---	---
<i>Vaccinium vacillans</i> .....	20	15	---	---	---
<i>Acer rubrum</i> .....	50	38	11	10	19
<i>Acer saccharum</i> .....	20	34	15	45	75
<i>Carya alba</i> .....	10	31	38	10	12
<i>Carya ovata</i> .....	20	38	22	30	25
<i>Cornus florida</i> .....	30	46	38	45	25
<i>Fraxinus lanceolata</i> .....	30	8	15	15	31
<i>Hydrangea arborescens</i> .....	10	23	11	5	37
<i>Nyssa sylvatica</i> .....	10	8	5	5	12
<i>Ostrya virginiana</i> .....	60	61	60	50	62
<i>Quercus alba</i> .....	10	46	60	45	19
<i>Quercus rubra</i> .....	70	77	55	60	50
<i>Sassafras variifolium</i> .....	60	62	60	50	62
<i>Vitis labrusca</i> .....	---	15	11	---	---
<i>Carya cordiformis</i> .....	---	8	---	---	6
<i>Quercus velutina</i> .....	---	46	15	20	---
<i>Fagus grandifolia</i> .....	---	15	27	60	56
<i>Sambucus canadensis</i> .....	---	---	5	---	---
<i>Fraxinus americana</i> .....	---	---	11	---	---
<i>Fraxinus pennsylvanicum</i> .....	---	---	11	---	---
<i>Morus rubra</i> .....	---	---	22	10	---
<i>Platanus occidentalis</i> .....	---	---	5	---	25
<i>Juglans cinerea</i> .....	---	---	11	5	6
<i>Cornus</i> sp? .....	---	---	11	15	6
<i>Ulmus americana</i> .....	---	---	5	15	37
<i>Prunus serotina</i> .....	---	---	---	5	---
<i>Ribes cynosbati</i> .....	---	---	---	5	---
<i>Liriodendron tulipifera</i> .....	---	---	---	5	6
<i>Ulmus fulva</i> .....	---	---	---	5	19
<i>Rubus allegheniensis</i> .....	---	---	---	10	19
<i>Carpinus caroliniana</i> .....	---	---	---	15	44
<i>Cercis canadensis</i> .....	---	---	---	---	19
<i>Rubus occidentalis</i> .....	---	---	---	---	12
<i>Acer negundo</i> .....	---	---	---	---	6
<i>Acer saccharinum</i> .....	---	---	---	---	6
<i>Benzoin æstivale</i> .....	---	---	---	---	6
<i>Celastrus scandens</i> .....	---	---	---	---	6
<i>Crataegus</i> sp? .....	---	---	---	---	6
<i>Fraxinus nigra</i> .....	---	---	---	---	6
<i>Gleditsia triacanthos</i> .....	---	---	---	---	6
<i>Juglans nigra</i> .....	---	---	---	---	6
<i>Pyrus coronaria</i> .....	---	---	---	---	6
<i>Smilax glauca</i> .....	---	---	---	---	6
Number of stations at each height (total 77) .....	10	13	18	20	16
Number of species at each height (total 45) .....	15	18	23	24	34

lists for the stations in each zone. Thus, in the hilltop section there are ten stations and *Populus grandidentata*<sup>1</sup> occurs in five of them, having a percentage, as listed, of 50 per cent; and so on through the whole table.

The number of species in each of the zones increases steadily from the top of the hills to the level of the river plain as follows: 15, 18, 23, 24 and 34, consecutively, in the five zones. It may be reasoned that the increase in number of species, or general richness of the flora, lower down may only be apparent and not real, since the number of stations is greater than at the top. The ratios between the number of stations and the number of species substantiate this argument except in the lowest zone, where the undoubted greater floristic richness is revealed in the presence of thirty-four species.

The distribution in the intermediate zones of the various species we must consider more a matter of chance, but there are certain species whose ecological characteristics are so marked that we may consider them as "hilltop" or "flood plain" species. For example, *Gaylussacia baccata* is confined to the top zone, while *Vaccinium vacillans* and *Populus grandidentata* are confined to the upper two zones. In some other work on the distribution of species (in relation to soil acidity and topography), Cain and Friesner (2) have called attention to the presence of these species and others on ridge tops and upper slopes, where they are considered "xerophytic-acid-boreal relics." In the lower flood plain zone there are twelve species which were not encountered elsewhere in this strip transect. Since the lower zone included more than the flood plain proper, it is not to be expected that these twelve species are strictly peculiar to the lower altitude. As a matter of fact, the strip transect fails to reveal the truly flood plain species as such, although one familiar with the trees of the region would know that of the twelve species, *Gleditsia triacanthos*, *Fraxinus nigra*, *Acer saccharinum* and *Acer negundo* are primarily flood plain and river bottom species. Two other species are worthy of note in this connection. *Ulmus fulva* and *Platanus occidentalis* are essentially flood plain species, although they frequently occur on lower slopes as here encountered.

Twelve species occur at all heights on these river hills from the bottom to the top of the ridges. They are *Acer rubrum*, *Acer saccharum*, *Carya alba*, *Carya ovata*, *Cornus florida*, *Fraxinus lanceolata*, *Hy-*

<sup>1</sup>Nomenclature after Gray's Manual, 7th Ed.

*drangea arborescens*, *Nyssa sylvatica*, *Ostrya virginiana*, *Quercus alba*, *Quercus rubra* and *Sassafras variifolium*. If we add to this list *Fagus grandifolia*, which occurred in all zones but the top, the list includes the most important woody species of the upland forest. In the particular region under study, the most characteristic species is *Quercus rubra*, ranging from the top of the hills to the bottom with the following high percentages: 70, 77, 55, 60 and 50 per cent, respectively.

Oak-hickory development is dominant here and in many places in Morgan county, but, given physiographic stability and freedom from the ax, the beech-maple climax will develop over the vast second-growth areas, as evidenced by many stands of almost pure beech-maple on a wide range of soils and slopes in the region. Most conspicuous among the small under-trees are *Ostrya virginiana* and *Sassafras variifolium*, each with a frequency of 50 per cent or over throughout the strip transect.

Of the twelve species ranging from the top to the bottom of the river hills, some occur with greater frequency on the lower slopes and some on the upper slopes. For example, *Acer saccharum*, as is true of its codominant, *Fagus grandifolia*, has a frequency of 20 per cent at the top and 75 per cent at the bottom of the hills. Other species show a greater tendency towards a higher frequency at the top of the hills, as *Acer rubrum*, with 50 per cent at the top and 19 per cent at the bottom. Still others are more common away from the extremes of the ridge tops and the flood plain, as *Quercus alba*, with percentages as follows: 10, 46, 60, 45, 19, respectively. As already suggested, floristic differences such as these are indicative of environmental differences, since species have more or less characteristic ecological requirements. The hilltops are considerably more xerophytic than the lower slopes and the flood plain; evaporation is greater as a result of higher temperatures and increased wind movement, while the soil is conspicuously better drained and, in the dry summer periods, becomes dry and crusted. In contrast, the flood plain is essentially hydrophytic, while the middle slopes represent more nearly the average mesophytism of the region, without the more extreme physiographic influences.

In conclusion, the strip method can be shown to have certain advantages. First, the data can be easily and rapidly obtained. The present transect was laid out in two short working days and the lists of species completed. Prerequisite, of course, is a familiarity with the species

encountered in such a survey, otherwise the time requirement would be greater. Secondly, the result of such a survey gives a considerably more definite idea of the vertical distribution of the woody species on the river hills than could be obtained by unaided observation.

### QUADRAT STUDY

When an attempt was made to determine the frequency of individual species in the woodland from the percentages derived by the strip transect studies (in the strict usage of the term "frequency"), it was found that the data were inadequate, although the strip was equivalent to about seventy-seven quadrats, twenty-five feet on a side, laid out in a line. Consequently, it was decided to go into the field again and collect data from the same region by the use of regularly spaced quadrats (or sample squares), for purposes of comparison with the strip transect method and to obtain true "frequency" data. The river hills were again divided into zones on a basis of height above the river. Seven zones were selected. The lowest flood plain zone ranged from the river level to fifteen feet above, while the second zone was from fifteen to fifty feet above the river. The first zone includes the flood plain proper. This subdivision separates the lower slope from the true flood plain, which was not the case in the first study. The other zones were fifty feet in height, except the top one, which was only fifteen feet in height. In each of these seven zones ten quadrats were laid out which were fifty feet on a side and regularly spaced from one another. In each of these quadrats (seventy in all) the total woody flora was listed. The results of this survey are presented in Table II.

The quadrat study revealed sixty-eight species, in contrast to forty-five species which were encountered in the strip transect survey. The number of different species encountered in the separate altitudinal zones is interesting in comparison with the first survey, where there was a steady increase in number of species in successively lower zones. Here the largest numbers of species were found to be in the intermediate regions. From top to bottom the number of species in each zone were as follows: 34, 36, 53, 40, 47, 44, 21. Apparently, fewer species can compete in the flood plain, where the drainage and aeration are poor during most of the year, and, conversely, relatively fewer species can compete with those adapted for life on the hilltops, where the soil becomes dry and baked during the hot summer season. This is a very

TABLE II

DISTRIBUTION AND FREQUENCY PERCENTAGE OF SPECIES ON A RIVER  
BLUFF. DATA FROM QUADRATS IN SEVEN ZONES

SPECIES	Height Classes in Feet Above the River							Average of All Quadrats
	250-285	200-250	150-200	100-150	50-100	15-50	0-15	
<i>Rhus copallina</i> .....	30	----	----	----	----	----	----	4
<i>Juniperus virginiana</i> .....	10	----	----	----	----	----	----	1
<i>Vaccinium vacillans</i> .....	30	20	20	----	----	----	----	10
<i>Viburnum acerifolium</i> .....	20	10	10	----	----	----	----	6
<i>Amelanchier canadensis</i> .....	20	10	10	----	----	----	----	6
<i>Populus grandidentata</i> .....	30	10	10	----	----	----	----	7
<i>Quercus velutina</i> .....	80	100	40	----	----	----	----	30
<i>Rubus odoratus</i> .....	20	70	20	20	----	----	----	19
<i>Nyssa sylvatica</i> .....	30	----	10	10	----	----	----	7
<i>Quercus alba</i> .....	60	40	40	40	20	----	----	29
<i>Carya alba</i> .....	20	10	40	20	10	----	----	14
<i>Fraxinus americana</i> .....	10	40	70	80	70	----	----	39
<i>Celastrus scandens</i> .....	40	20	30	----	10	----	----	14
<i>Acer saccharum</i> .....	100	100	100	100	100	100	----	86
<i>Sassafras variifolium</i> .....	100	80	70	50	80	90	----	67
<i>Rubus allegheniensis</i> .....	70	40	40	10	20	70	----	36
<i>Hydrangea arborescens</i> .....	60	80	30	40	40	40	----	41
<i>Carya ovata</i> .....	60	50	60	40	40	20	----	39
<i>Quercus rubra</i> .....	60	50	90	50	50	70	----	53
<i>Acer rubrum</i> .....	60	30	40	----	20	30	----	26
<i>Fagus grandifolia</i> .....	40	60	70	30	90	50	----	49
<i>Ostrya virginiana</i> .....	40	80	80	50	60	40	----	50
<i>Rubus occidentalis</i> .....	40	10	30	10	30	50	----	24
<i>Prunus serotina</i> .....	30	----	10	10	50	60	----	23
<i>Ulmus fulva</i> .....	30	50	20	50	40	80	----	37
<i>Morus rubra</i> .....	20	40	60	80	40	70	----	44
<i>Evonymus atropurpureus</i> .....	10	----	30	20	20	20	----	14
<i>Liriodendron tulipifera</i> .....	10	20	20	20	50	50	----	24
<i>Vitis labrusca</i> .....	80	50	90	70	90	50	20	64
<i>Rhus toxicodendron</i> .....	60	50	90	70	100	60	70	71
<i>Cornus florida</i> .....	60	100	80	60	80	50	10	63
<i>Fraxinus lanceolata</i> .....	60	80	90	50	70	90	70	73
<i>Carya cordiformis</i> .....	10	30	20	40	60	70	10	34
<i>Tilia americana</i> .....	10	60	30	10	----	10	10	19
<i>Fraxinus quadrangulata</i> .....	10	30	----	10	----	----	----	7
<i>Juglans cinerea</i> .....	20	60	20	70	40	----	----	30
<i>Ulmus americana</i> .....	20	30	50	70	20	----	----	27
<i>Celtis occidentalis</i> .....	40	40	20	30	100	----	----	33
<i>Æsculus glabra</i> .....	10	10	20	10	50	----	----	14
<i>Asimina triloba</i> .....	20	40	50	60	50	10	----	33
<i>Sambucus canadensis</i> .....	10	20	10	40	50	30	----	37
<i>Quercus coccinea</i> .....	----	10	----	----	----	----	----	1
<i>Prunus virginiana</i> .....	----	10	----	----	----	----	----	1
<i>Gymnocladus dioica</i> .....	----	40	20	----	----	----	----	9
<i>Crategus</i> sp?.....	----	10	20	50	----	----	----	11
<i>Benzoin æstivale</i> .....	----	40	30	40	30	----	----	20
<i>Juglans nigra</i> .....	----	30	10	----	60	----	----	14
<i>Cercis canadensis</i> .....	----	30	30	50	60	----	----	24
<i>Rhus glabra</i> .....	----	20	----	10	20	----	----	6

SPECIES	Height Classes in Feet Above the River							Average of All Quadrats
	250-285	200-250	150-200	100-150	50-100	15-50	0-15	
<i>Carpinus caroliniana</i> .....	----	----	10	70	50	60	20	30
<i>Smilax glauca</i> .....	----	----	20	----	60	60	10	36
<i>Rosa setigera</i> .....	----	----	10	----	20	40	10	11
<i>Gleditsia triacanthos</i> .....	----	----	40	----	10	10	20	11
<i>Acer negundo</i> .....	----	----	20	20	60	70	60	33
<i>Platanus occidentalis</i> .....	----	----	10	30	20	40	70	24
<i>Quercus macrocarpa</i> .....	----	----	----	10	----	30	----	6
<i>Betula nigra</i> .....	----	----	----	----	10	----	----	1
<i>Hamamelis virginiana</i> .....	----	----	----	----	10	----	----	1
<i>Ribes cynosbati</i> .....	----	----	----	----	10	30	----	6
<i>Quercus muhlenbergii</i> .....	----	----	----	----	10	30	----	6
<i>Acer nigrum</i> .....	----	----	----	----	10	30	10	7
<i>Ulmus racemosa</i> .....	----	----	----	----	10	80	70	23
<i>Fraxinus nigra</i> .....	----	----	----	----	----	30	----	4
<i>Cornus</i> sp?.....	----	----	----	----	----	40	20	9
<i>Acer saccharinum</i> .....	----	----	----	----	----	----	100	14
<i>Salix nigra</i> .....	----	----	----	----	----	----	70	10
<i>Populus deltoides</i> .....	----	----	----	----	----	----	60	9
<i>Tecoma radicans</i> .....	----	----	----	----	----	----	20	3
Quadrats in each belt.....	10	10	10	10	10	10	10	----
Species in each belt.....	34	36	53	40	47	44	21	----
(Total 68)								

widespread and well-known ecological situation: the more rigorous habitats, whether dry or wet, characteristically have fewer species than the intermediate typically mesophytic habitats.

Essentially the same species were found by the quadrat study to characterize the hilltops, but the more extensive quadrat survey reveals three new characteristic species, *viz.*, *Rhus copallina*, *Juniperus virginiana* and *Amelanchier canadensis*.

The flood plain proper was found to contain twenty-one woody species, of which four were encountered nowhere else. They are *Acer saccharinum*, *Populus deltoides*, *Salix nigra* and *Tecoma radicans*. Five additional species occur in 60-70 per cent of the flood plain quadrats: *Fraxinus lanceolata*, *Rhus toxicodendron*, *Platanus occidentalis*, *Acer negundo* and *Ulmus racemosa*.

In a quadrat survey, the question of frequency of species and the indication of dominants are among the interesting results. In their admirable "Vocabulaire de Sociologie Vegetale," third edition, Braun-Blanquet and Pavillard (1) have this to say about "frequency" (freely translated):

"Frequency is a statistical idea (expression) which is derived by complete floristic lists from a certain number of sample areas (quad-

rats) of equal dimensions and disseminated as much as possible throughout the extent of the individual example of the association. The *frequency* of a species is then expressed in per cent by the relation between the number of quadrats which contained it and the total number of areas analyzed in the particular example of the association.

"The species are then usually divided into five *Classes of Frequency*, according to their percentages."

Strictly speaking, "dominance" is also a matter of degree, yet certain most characteristic species of considerable coverage are often referred to as "dominants." In Braun-Blanquet and Pavillard's vocabulary we find:

"To evaluate *dominance* one must be able to assign figures to each species with the exact significance as follows: 1, covering very slightly; 2, species covering between  $1/20$  and  $1/4$  of the area of the association; 3, species covering between  $1/4$  and  $1/2$  of the surface; 4, species covering between  $1/2$  and  $3/4$  of the surface, and, 5, species covering more than  $3/4$  of the surface."

Very little work has been done in the United States which would enable the investigators to assign degrees of dominance in this manner. Increasing attention should be paid to the methods of quantitative statistical analysis of vegetation which have been developed in the various European schools of ecology. Many American ecologists have followed the practice of referring to species of "high" frequency as "dominants," whereas, a species may be present in 100 per cent of the quadrats laid out in an association and still not be dominant because of its low surface coverage. The conception of which species are dominant is usually derived by observation unaided by the quantitative statistical methods of plant sociology. Our present field data do not permit the exact reference to any species as dominants, since the extent of coverage of each species in each quadrat was not determined. However, when we find, for example, that *Acer saccharum* has 100 per cent frequency in all zones except the flood plain, it must also be dominant.

There are certain other words which are constantly used in descriptions of vegetation which have come to have technical definitions and consequently should not be used laxly any longer. Three such words which might be appropriately considered here are *presence*, *constance* and *fidelity*. Returning again to the vocabulary cited above, we read: "*Presence* is established according to the existence or absence of a species in different examples (geographically separated) of an associa-

tion. Certain species are met with a high regularity in all or nearly all the examples of an association encountered; others are lacking in a more or less large number. One can divide them into categories according to different degrees of presence. The *Constance* is an expression relative to presence, referring to selected samples of definite dimensions, but large enough, taken only once in each different stand of the association. In combining the results of constance with frequency, one obtains a synthetic expression of the distribution, more or less uniform, of the species in the different individual examples of the association. It is said to be an expression, more or less approximate, of the homogeneity of the association." *Fidelity* is considered as the extent to which species are confined to a particular plant association, or type of plant community.

In view of these concepts, if we consider the flood plain as a distinct association, four species have a complete fidelity, in that they are confined to the flood plain association in this particular survey. They are *Acer saccharinum*, *Salix nigra*, *Populus deltoides* and *Tecoma radicans*. Similarly, considering the upper slope and hilltops to be covered with a black oak association, above about two hundred feet, we find seven species with a high degree of fidelity, viz., *Quercus velutina*, *Populus grandidentata*, *Amelanchier canadensis*, *Viburnum acerifolium*, *Vaccinium vacillans*, *Juniperus virginiana* and *Rhus copallina*. The latter two are confined to the topmost zone.

In order to determine constance and presence in the strict technical use of the terms, surveys such as this one would have to be made in other localities where similar associations and situations are to be found. We have here only one instance or example of these river hill associations—one "stand," in the terminology of the foresters.

In a consideration of frequency, only quadrats laid out within the typical portion of the association (of a single association) can be considered in determination of frequency of species. Consequently, our first zone, from the river to fifteen feet above, which includes only the flood plain, must be considered separately and the frequency for the twenty-one species contained therein determined. The results are presented in Table III.

The frequency indices of the various species in the flood plain coincide with the normal expectancy in such work when the conditions of such study are fulfilled: a sufficient number of quadrats of sufficient area distributed throughout the association. That this analysis is ade-

TABLE III  
FREQUENCY CLASSES OF THE SPECIES OF THE FLOOD  
PLAIN ASSOCIATION

SPECIES	Raunkiaer's Frequency Classes				
	A 0-20%	B 21-40%	C 41-60%	D 61-80%	E 81-100%
<i>Acer nigrum</i> .....	x				
<i>Asimina triloba</i> .....	x				
<i>Carpinus caroliniana</i> .....	x				
<i>Carya cordiformis</i> .....	x				
<i>Cornus</i> sp? .....	x				
<i>Cornus florida</i> .....	x				
<i>Gleditsia triacanthos</i> .....	x				
<i>Rosa setigera</i> .....	x				
<i>Smilax glauca</i> .....	x				
<i>Tecoma radicans</i> .....	x				
<i>Tilia americana</i> .....	x				
<i>Vitis labrusca</i> .....	x				
<i>Sambucus canadensis</i> .....		x			
<i>Populus deltoides</i> .....			x		
<i>Acer negundo</i> .....				x	
<i>Fraxinus lanceolata</i> .....				x	
<i>Platanus occidentalis</i> .....				x	
<i>Rhus toxicodendron</i> .....				x	
<i>Salix nigra</i> .....				x	
<i>Ulmus racemosa</i> .....				x	
<i>Acer saccharinum</i> .....					x
Number of species (21).....	12	1	1	6	1

quate may be decided from a comparison of the results with standard frequency work. Kenoyer (3) has made a critical study of the frequency work, first developed by Raunkiaer (5). Raunkiaer, working on European associations, found that the species in an association, when arranged into five frequency classes, had the following grouping: Class A (1-20 per cent of the quadrats), 53 per cent of the total number of species encountered; Class B (21-40 per cent), 14 per cent of the species; Class C (41-60 per cent), 9 per cent of the species; Class D (61-80 per cent), 8 per cent of the species, and Class E (81-100 per cent), 16 per cent of the species. In other words, there were two peaks in frequency. First, there was a large percentage of the species which were of low frequency (Class A) being encountered in 20 per cent or less of the quadrats. Second, there was another peak, or large percentage of the species which were of high frequency (Class E), being encountered in 81 per cent or more of the quadrats. This second peak is never as high as the former; in other words, there are fewer species of high frequency than there are of low frequency in an association. The smallest frequency class is usually Class D, although it may be Class

C. Raunkiaer's ratio of frequency classes, 53-14-9-8-16, was derived from an extensive study involving 8,087 percentages.

The work of Kenoyer on American association gives the following ratio: 69-12-6-4-9, showing the same two high points with the difference, as Kenoyer explained, that Class A is larger in American associations, due to the fact that our flora is generally richer in numbers of species.

The flood plain association, from the present analysis, gave the following ratio: Class A, 57 per cent; Class B, 5 per cent; Class C, 5 per cent; Class D, 28 per cent, and Class E, 5 per cent, revealing the two large frequency classes mentioned above. Generally speaking, when the two classes of large size are at either end of the scale, it may be concluded that the number and size of the quadrats is adequate and that a homogeneous association has been dealt with.

Next we have to consider the wooded slopes of the river hills above the flood plain. These woods are not virgin timber, yet they are relatively undisturbed in comparison to the majority of timbered areas in central Indiana and would be described generally as mixed hardwoods. The hilltops and upper slopes are occupied by what is more nearly an oak-hickory association, while the lower slopes are clothed with a more mesophytic growth, approaching the beech-maple association. The normal woodland succession is usually from the more xerophytic oak-hickory association, with black and red oak playing important roles in the makeup of the vegetation, followed by a white oak stage with an admixture of more mesophytic species, which finally gives way to the beech-maple climax association. The succession, developing towards the beech-maple association, is further along on the lower slopes than on the upper slopes and ridge tops. This can be seen from the following percentages of critical species, Table IV:

TABLE IV

FREQUENCY OF MORE IMPORTANT SPECIES OF THE OAK AND  
BEECH-MAPLE ASSOCIATIONS

SPECIES	Frequency Per Cent by Altitudinal Zones						
	250-285	200-250	150-200	100-150	50-100	15-50	0-15
<i>Quercus velutina</i> ....	80	100	40	----	----	----	----
<i>Quercus rubra</i> .....	60	50	90	50	50	70	----
<i>Quercus alba</i> .....	60	40	40	40	20	----	----
<i>Carya ovata</i> .....	60	50	60	40	40	20	----
<i>Carya alba</i> .....	20	10	40	20	10	----	----
<i>Fagus grandifolia</i> ....	40	60	70	30	90	50	----
<i>Acer saccharum</i> .....	100	100	100	100	100	100	----

TABLE V  
FREQUENCY CLASSES OF THE HILLTOP SPECIES

SPECIES	Frequency Classes				
	A 0-20%	B 21-40%	C 41-60%	D 61-80%	E 81-100%
<i>JEsculus glabra</i> .....	x				
<i>Amelanchier canadensis</i> .....	x				
<i>Asimina triloba</i> .....	x				
<i>Carya alba</i> .....	x				
<i>Carya cordiformis</i> .....	x				
<i>Celtis occidentalis</i> .....	x				
<i>Evonymus atropurpureus</i> .....	x				
<i>Fraxinus quadrangulata</i> .....	x				
<i>Juglans cinerea</i> .....	x				
<i>Juniperus virginiana</i> .....	x				
<i>Liriodendron tulipifera</i> .....	x				
<i>Nyssa sylvatica</i> .....	x				
<i>Populus grandidentata</i> .....	x				
<i>Prunus serotina</i> .....	x				
<i>Rhus copallina</i> .....	x				
<i>Sambucus canadensis</i> .....	x				
<i>Ulmus americana</i> .....	x				
<i>Viburnum acerifolium</i> .....	x				
<i>Celastrus scandens</i> .....		x			
<i>Fraxinus americana</i> .....		x			
<i>Morus rubra</i> .....		x			
<i>Rubus occidentalis</i> .....		x			
<i>Tilia americana</i> .....		x			
<i>Ulmus fulva</i> .....		x			
<i>Vaccinium vacillans</i> .....		x			
<i>Acer rubrum</i> .....			x		
<i>Carya ovata</i> .....			x		
<i>Fagus grandifolia</i> .....			x		
<i>Ostrya virginiana</i> .....			x		
<i>Quercus alba</i> .....			x		
<i>Quercus rubra</i> .....			x		
<i>Rubus odoratus</i> .....			x		
<i>Rubus allegheniensis</i> .....			x		
<i>Rhus toxicodendron</i> .....			x		
<i>Cornus florida</i> .....				x	
<i>Fraxinus lanceolata</i> .....				x	
<i>Hydrangea arborescens</i> .....				x	
<i>Vitis labrusca</i> .....				x	
<i>Acer saccharum</i> .....					x
<i>Quercus velutina</i> .....					x
<i>Sassafras variifolium</i> .....					x
No. of species (41).....	18	7	9	4	3
Percentage .....	44	17	22	10	7

The hilltops being more nearly representative of the oak-hickory association, the upper two zones (from 200 to 285 feet) were treated so as to reveal the frequencies of the species. These results are expressed in Table V. The ratio of the classes here revealed is not that

of the typical Raunkiaerian type. The second peak, represented by the large size of Class E, is absent in the results: 44-17-22-10-7. The conclusion to be drawn, and which had already been anticipated, is that the plant community here dealt with is not a good homogeneous example of the oak-hickory association. Similarly, the lower slopes are approaching the beech-maple association but are not yet typically developed, for, if such were the case, the frequency results would reveal the "dominants" as composing Class E, and also constituting a second peak, *i. e.*, more species falling into Class E than in Class C or D.

## SUMMARY

1. This report covers analyses of the woody vegetation of certain central Indiana river hills by two methods: (1) strip transect method; (2) quadrat method, with a discussion of the advantages of each in revealing the content and distribution of the woody flora.

2. The vertical distribution of the species is emphasized, in relation to habitat factors, by a treatment involving altitudinal zones.

3. The question of frequency of the species is considered and certain terms used in plant sociology are discussed.

4. The use of Raunkiaer's and Kenoyer's ratios of frequency classes is considered as to their value in checking the adequacy of the quadrat survey, and whether or not the plant community dealt with is a good example of the association under consideration.

5. The present study is of academic interest only, but many problems of practical importance involve methods of analysis of vegetation here discussed.

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# CERTAIN ASPECTS OF THE H-ION CONCENTRATION OF THE SOILS OF A CENTRAL INDIANA RIVER BLUFF

By STANLEY A. CAIN AND RAY C. FRIESNER

In a recent paper, Cain and Friesner (3) found that there was a relation between topography and the hydrogen-ion concentration of the soil. This work was done on certain hills in the Sycamore creek region, Morgan county, Indiana, where it was found that the acidity was greater on the hilltops and less in the intervening ravines, so that curves representing the degree of acidity of the soil at different points on a line crossing the hills were roughly parallel with the topography. The average acidity on three ridge tops was pH 5.3, while the adjacent ravine bottoms were practically neutral, averaging pH 6.9. The consistently greater acidity of the ridge tops and upper slopes seems to play a significant part in the distribution of certain plants found only in such situations, viz., *Vaccinium vacillans*, *Gaylussacia baccata*, *Polyptrichum juniperinum*, etc. Since these ridges studied in the Sycamore creek region were only about one hundred feet high, it was thought desirable to investigate some river hills which rise about 250 feet above their immediate bases.

The work reported in this paper was also made in Morgan county, Indiana, at a point on White river known as Blue Bluffs. The soil samples for the pH investigation were taken in connection with a transect study of the vegetation, Cain, *et al.* (4). Surface and subsoil samples were taken at twenty-five-foot intervals, starting at the bank of the river in a line running 650 feet directly to the top of a hill known locally as Rock Hill. The steepest part of the slope is near the summit of the hill. At the top of the hill the line on which the samples were taken turned 45 degrees to the west and descended into a ravine, where it continued westward to the top of Blue Bluffs. The total length of the line was 1,925 feet, and the soil samples consisted of seventy-seven sets, each set comprising a surface sample and one taken at a depth of six inches. It has seemed advisable to arrange the results in six groups, on a basis of the altitude above the river level of the place where each soil sample was taken. Thus the lowest group of soil samples, from the river level to fifteen feet above the river, included the region of the flood

plain species. Similarly, the last group of samples, from 200 to 285 feet above the river, was in the region of what may be called the "hill-top" species.

Weaver and Clements (6), in their new ecology text, remark that, "It is frequently desirable to know just how vegetation varies with changing environment, such as caused by slope, exposure or other irregularities in topography or soil." In completely wooded river bluffs like the ones here considered, differences in evaporation are probably not great between the tops and bottoms of the hills. Edaphic factors are undoubtedly of greater importance in effect on the vegetation. Soil moisture conditions and the physical and chemical nature of the soil seem to be quite different and need to be investigated. It is the opinion of the present writers that many of the more commonplace and obvious ecological situations need quantitative investigation, if not for substantiation of our preconceived ideas, at least for classroom work. The following results of our pH determinations are a step in that direction.

## RESULTS

The results of 477 tests of the pH of the soils are summarized in Table I.

TABLE I

AVERAGE pH OF SOIL SAMPLES TAKEN AT DIFFERENT ALTITUDES ON  
ROCK HILL AND BLUE BLUFFS

Altitude Class	Surface Soils		Subsoil Samples	
	No. of Samples	pH	No. of Samples	pH
200-285 ft. (Hilltop).....	10	5.89	10	5.13
150-200 ft. ....	13	5.76	13	4.73
100-150 ft. ....	18	5.65*	18	4.93*
50-100 ft. ....	20	5.79*	20	4.94*
15- 50 ft. ....	8	5.9	8	5.0
1- 15 ft. (Flood plain).....	8	6.5	8	5.8

\*These averages were obtained by omitting three soil samples which were involved in a local land-slump, where the surface and subsoil were mixed up.

Wherry (7) has recently called attention to the necessity of realizing the logarithmic nature of the pH numbers when they are averaged, since the direct averaging of them may result in considerable error. If the H-ion concentration is not to be expressed in terms of "active acidity," it is necessary to average them on that basis and change them back to the more familiar pH numbers afterwards. This has been done in preparing the averages in Table I.

This investigation does not reveal as close an adherence of the pH to the topography as was found in our earlier work in the Sycamore creek region, yet the slopes are more acid than the flood plain. These figures can be taken as a certain additional substantiation of the general fact of leaching out of upland soils and the subsequent increase in the acidity, Salisbury (5). In these soils the acidity is conspicuously greater at a depth of six inches than immediately beneath the surface litter. This situation is undoubtedly due to the chemical nature of the parent material of the subsoil, although no analyses or geological study have been made as yet of the region from this point of view. It seems that a more widespread condition is that where the surface soils are more acid than the subsoils, Salisbury (5), Cain (1) (2), Cain and Friesner (3), etc. This condition is ordinarily a result of the accumulation of organic material yielding humus acids at the surface and the leaching out of bases which are not replenished as are the acids.

It has been the policy in our work to date to make three tests of the hydrogen-ion concentration of each soil sample. The Youden portable apparatus, permitting rapid determinations of the e.m.f. of the soil solutions, has been used for the tests. It was found that the average deviation of the three tests made on each sample was approximately 0.1 pH. The deviations are condensed on a basis of the degree of the acidity in Table II.

TABLE II  
AVERAGE DEVIATIONS FROM THE MEAN OF THREE TESTS ON EACH  
SOIL SAMPLE

pH Range	Deviation from Mean	Number of Samples	Number of Tests
pH 7 range.....	0.0935	6	18
pH 6 range.....	0.1253	28	84
pH 5 range.....	0.1302	59	177
pH 4 range.....	0.0995	49	147
Grand average .....	0.117	142	426

There seems to be no special correlation between the degree of deviation of three tests on a sample and the degree of the acidity. The greatest deviation from the mean of three tests was found in surface soil No. 111, with a range from pH 5.306 to 5.969, and in subsoil No. 118, ranging from pH 5.867 to 6.615, or 0.33 and 0.37 respectively.

## SUMMARY AND CONCLUSIONS

1. A total of 477 tests were made of the hydrogen-ion concentration of the soils on a line running 1,925 feet over two river hills, Blue Bluffs and Rock Hill.

2. There were 79 sets of surface and subsoil samples, 77 of which were on the line mentioned above.

3. In 90 per cent, or 71 of the 79 sets (three tests per sample), the subsoil was more acid than the surface soil by an average of approximately 0.8. Most of the eight exceptions were connected with a landslide which would account for the disturbance of the normal stratification.

4. For all the sets of surface and subsoils the range was from pH 4.4 to 7.7, and from pH 4.3 to 7.4 respectively.

5. For all samples the average reaction of the surface soil was pH 5.9 and the subsoil pH 5.1.

6. The greatest difference between the reaction of the surface soil and the subsoil of any one set was from pH 4.7 (subsoil) to pH 7.5 (surface soil). The least difference was from pH 4.45 to 4.47.

7. The average deviation from the mean of three tests on a soil sample was approximately 0.1, a factor sufficiently small to obviate the necessity of duplicate tests on individual soil samples. It is apparent, however, that numerous soil samples must be read in order to gain any accurate idea of the characteristic reaction of the soil of a particular situation or vegetation type.

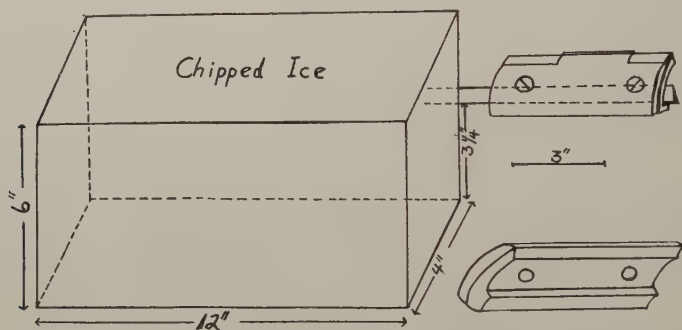
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# A MICROTOME KNIFE COOLER

By RAY C. FRIESNER

Artschwager<sup>1</sup> described a cooling apparatus for handling paraffin ribbons during hot weather. Use of this device in our laboratory during the summer months has proven highly satisfactory and at the same time it suggested to us the idea of using the same principle to keep the knife blade cool while cutting. Accordingly, a copper box was made 12x6x4 inches, as shown in the accompanying figure. A suitable lid should be made from the same material. On the back of this box was



soldered a narrow strip of copper, which was allowed to project approximately seven inches beyond the end of the box. This projecting strip should be just wide enough to fit into the groove on the back of the blade holder of the microtome, which happens to be just one-half inch in the case of the blade holder used in our laboratory.<sup>2</sup> It should be soldered to the back of the box just high enough from the bottom to permit it to slide easily into the blade holder groove when the holder is in place on the microtome. This height is just three and nine-sixteenths inches for our Spencer Rotary microtome.

When ready for use, the copper box is filled with chipped ice, to which sodium chloride may be added to increase the cooling effect. The lid is then placed on the box and the low temperature is then rapidly conducted through the extending arm to the microtome blade holder, which is made of brass. This device has permitted paraffin cutting to be done throughout the summer session and on the very hottest of days.

<sup>1</sup>Artschwager, Ernest. A Paraffin Ribbon Cooler. *Stain Tech.* 1: 112. 1926.

<sup>2</sup>Made by Mr. Ralph B. Larsen, 7126 Woodlawn Ave., Chicago.



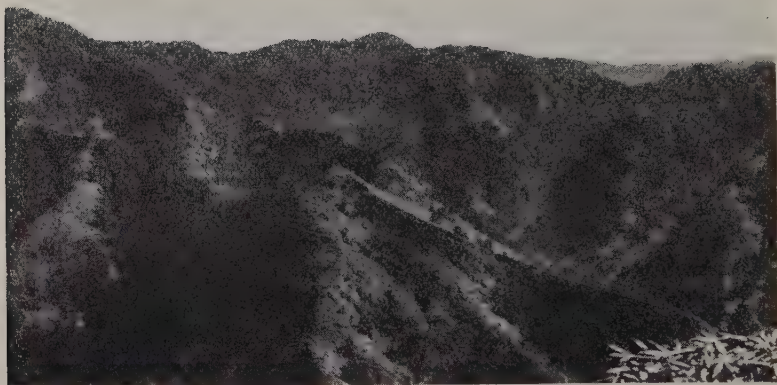


Figure 1. Ridge-type heath balds in the spruce-fir subalpine zone, between Mt. LeConte and the North Carolina-Tennessee state line, Great Smoky mountains. Photograph by courtesy of Jim Thompson Co., Knoxville.



Figure 2. Detail of vegetation at the margin of a heath bald of the type illustrated in Figure 1, at approximately 6,500 feet elevation on Mt. LeConte.

# AN ECOLOGICAL STUDY OF THE HEATH BALDS OF THE GREAT SMOKY MOUNTAINS

*By* STANLEY A. CAIN

The inhabitants of the Great Smoky mountains usually refer to the heath communities under consideration as "slicks" or "balds." The former name is derived from the smooth appearance they present on the ridges and mountain tops when viewed from a distance and which is entirely misleading, for they are extremely rough and tangled. The name "bald" refers to the absence of trees, these areas being exclusively occupied by shrubs. The term "heath bald" is used in this paper to include all such treeless areas dominated by members of the order Ericales. The use of the term "heath" is not entirely satisfactory, since there is considerable confusion in the literature in respect to the exact meaning of such terms as "heath," "low moor," "high moor," etc., yet no substitute for the term has been found.

One derives from Tansley, in "Types of British Vegetation," that heathland involves poor, dry, sandy soils, usually with a thin layer of dry peat or "trochentorf." The climate can best be described as oceanic where heathland is characteristic, and where the rainfall is greater, up to forty and sixty inches, relatively pure acid humus may develop to a foot in depth. This type of community is considered by Warming (23) under the heading "Dwarf Shrub Heath," where he says that in the Alps, associated with the forest and above the timber line, heaths are formed by various plants, and that in Azalea-heath the layer of raw humus may attain a thickness of half a meter. In distinction to Tansley, Warming considers the production of raw humus as the most characteristic peculiarity of heath, while they agree in respect to the climatic conditions. Warming states that the "dwarf shrub heath occurs only in arctic and alpine sites, also in the oceanic west coasts of the cold-temperate zone that are characterized by cool summers."

In the Great Smoky mountains, areas of heath are to be found with a development of dry peat, particularly at lower altitudes, but the majority of the heath balds have a remarkable development of moist, fibrous brown peat, frequently to a depth of one and two feet. The surface of the peat under the ericaceous shrubs is frequently covered

with a dense mat of *Sphagnum* and other peat-forming mosses. Other species of moss and lichens, as *Cladonia* and *Usnea*, may be festooned over the branches, particularly when the balds are at an elevation of 6,000 feet or more.

The presence of peat-forming mosses suggests the possible application of the term "moor" or "high-moor" to these areas. Warming (23), page 200, says: "The moor known as high-moor, *Sphagnum*-moor or heather-moor, is mainly formed by bog-moss (*Sphagnum*) and arises on moist soil, which is only slightly permeable to water, though very damp air hangs over it. Humid air and dew are essential to sphagnum-moor, which acquires the whole of its moisture from atmospheric precipitations. It often arises on top of old low-moor; it may also take origin on wet sand, and even on rocks if these be frequently wet, as on the west coast of Norway and Sweden." Thus it would seem that the distinction between moor and heath rests on the presence or absence of *Sphagnum*; yet heather-moor and dwarf shrub heath, from descriptions, are frequently indistinguishable. However, the following differences between the peat-forming areas of the Great Smoky mountains and true high-moor occur to the writer as distinguishing the two: (1) the high-moor has a convex surface like a watch glass (the sort of thing known as "raised bog" in this country); (2) the high-moor is characterized by the presence of "carnivorous" plants. Altogether, the term "heath bald" seems preferable to "moor" in this connection.

The term "pine-heath," or kiefern-heide, is not subject to the same confusion, since the pines are associated with the heath shrubs under conditions too dry for *Sphagnum* and the formation of moist brown peat. Harshberger (19 and 20), in describing the New Jersey Pine Barrens, says that "pine-heath is found where the climate is continental." In comparison with the climate of the heath districts, the pine-heath regions are marked by increase in range of annual and diurnal temperatures, rainfall is less, skies are more frequently cloudless and the air is drier and dustier. In the Great Smoky mountains the pine-heath is quite constant in aspect, but the heath balds show a number of facies, the principal variations of which are tied up with changes concomitant with increased altitude.

## DISTRIBUTION OF HEATH BALDS AND PINE-HEATH IN THE GREAT SMOKY MOUNTAINS OF NORTH CAROLINA AND TENNESSEE

The principal region of heath balds is in the vicinity of the North Carolina-Tennessee state line, from Laurel Top along the Sawtooth range to Mt. Collins, westward on Mt. LeConte and the intervening territory, and southwestward to the limits of the spruce. In this region, in the very heart of the roughest mountains of the area, are to be found the steep ridges and peaks, barren of trees, yet clothed with the densest imaginable growth of ericaceous shrubs. Mt. Guyot to the northeast and Clingman's Dome to the southwest, the two highest peaks in the Great Smoky mountains, approximately mark off this region of numerous heath balds of the type under consideration. These two mountains are themselves essentially without such areas, a phenomenon probably related to their more bulky and less precipitous form. Below Clingman's Dome the heath balds are less frequent until in the southwestern part of the Great Smoky mountain National Park area, from Thunderhead mountain to the Little Tennessee river, they are entirely absent, being replaced by grassy balds. This lower, more southern region is also without the spruce-fir formation which stops south of Clingman's Dome about at Double Spring Gap. To the north and east the heath bald is to be found in varying frequency and character as far at least as the Craggy mountains, where they have been described by Davis (5). The present work has, in the main, been done in the vicinity of Mt. LeConte, because of greater accessibility, although excursions have been made to all parts of the range.

The heath balds are to be found at the tops of ridges and peaks with all exposures and with varying degrees of slope. It has not been possible to correlate the balds with southern exposure, for example, or merely with the angle of slope, although the latter may sometimes be an important factor. They may occur merely as narrow strips along knife-edge ridges, as on Beartrap lead or the Alum Cave balds, or they may occupy the top and extensive upper slopes of a mountain, as in the case of Brushy mountain north of Mt. LeConte.

The pine-heaths occur generally at lower elevations than the heath balds and in many respects occupy comparable positions. Pine-heath is particularly abundant between 3,000 and 4,000 feet in elevation on south exposures. In such situations the pine-heath frequently extends

to the top of the mountain or ridge, as in the case of Piney mountain or Bullhead, where there is an extremely sharp line of transition to chestnut or oak forest. Down the slope on all sides these pine and hardwood forests merge gradually into the so-called "cove" forests of greater luxuriance and productiveness.

#### DESCRIPTION OF THE VEGETATION OF HEATH BALDS: SPECIES CONTENT AND RELATION TO SURROUNDING FORESTS

Before pointing out the peculiarities of the heath balds and their relationship to the adjacent forest types, it will be necessary to consider briefly the major aspects of the vegetation of the region as a whole. The vegetation areas of the Great Smoky mountains present some confusion when classifications are attempted, especially on a single basis.

The major distinctions should be apparent and consist of climatically controlled vegetational units capable of reproducing themselves and consequently resulting in various dynamic subdivisions related to many factors, yet tending always towards the climax condition of relative stability. This concept of major divisions of vegetation, as established by Schimper and adequately presented recently in Weaver and Clement's (24) *Plant Ecology*, provides for only two formations in the region of the Great Smoky mountains, namely:

Subalpine Forest: *Picea-Abies* Formation.

Deciduous Forest: *Quercus-Fagus* Formation.

The *Picea-Abies* formation is easily disposed of, since it has a remarkable floristic homogeneity. In Tennessee and North Carolina, or in New England or Southern Canada, it is essentially the same. It is not so with the deciduous forest, which has been variously handled by ecologists and foresters. Weaver and Clement's subdivisions are as follows:

##### *Deciduous Forest: Quercus-Fagus Formation*

1. Maple-beech forest: *Acer-Fagus* association.
2. Oak-chestnut forest: *Quercus-Castanea* association.
3. Oak-hickory forest: *Quercus-Hicoria* association.
  - a. Pine subclimax: *Pinus* associes.

The Committee on Forest Type Classification, Frothingham, *et al.* (8), have given us the following convenient grouping for the forest types of the Southern Appalachians:

Northern Forest (mostly at high altitudes)—1, Spruce-fir type; 2, Hemlock-yellow birch type; 3, Northern hardwood type.

Moist Slope and Cove Forest—4 to 11 (types based on importance of different species).

Dry Slope and Ridge Forest—12, Chestnut oak type; 13, Black oak-scarlet oak type; 14, Pitch pine-mountain pine type.

The following tabulation (Table I) presents the flora of the heath balds with an indication of the forest type with which each species is most frequently associated. The column numbers in the tabulation indicate the following main types selected from the above classifications: (1) Spruce-fir forest, (2) Northern hardwoods forest, (3) Upper cove forest, (4) Chestnut-oak forest, and (5) Pine-heath (pine subclimax).

The preceding table emphasizes a number of points about the flora of the heath balds. In the first place, it is striking that there are so few species. The observations on which these results are based were made during four years, in early spring and from June to middle September. At no time is there any display of herbaceous elements, although numbers of these heath balds were visited during this time. The flora is conspicuously woody, 74 per cent. As shown in the tabulation, 47 per cent of the woody flora is found in one family, Ericaceæ, which includes all the dominants.

Since heath balds occur at all altitudes from 4,000 feet to 6,500 feet, it would be expected that the species content would vary somewhat with altitude. This is the case, and not only are some of the species different in the heath balds at Myrtle Point and Main Top, at about 6,500 feet on Mt. LeConte, but the relative abundance and dominance of certain species, common to them and to balds at lower elevations, are different. The flora of balds occurring at higher elevations is distinctly related to the spruce-fir formation. On the other hand, the balds at lower elevations, like Ball mountain and Bullhead mountain, show definite relation to chestnut-oak and pine-heath associations. Intermediate situations like Chimney Caps, Buffalohead, Scratch-britches, etc., are more nearly related to the cove forests and the northern hardwoods.

TABLE I

FLORA OF THE HEATH BALDS AND RELATION OF SPECIES TO PRINCIPAL FOREST TYPES<sup>1</sup>

FLORA	Forest Types					FLORA	Forest Types				
	1	2	3	4	5		1	2	3	4	5
Polypodiaceæ						Aquifoliaceæ					
<i>Pteris aquilina</i> .....				x	x	<i>Ilex monticola</i> .....		x			
<i>Aspidium spinulosum</i>						Aceraceæ					
intermedium .....	x					<i>Acer rubrum</i> .....		x			
<i>Dicksonia puncti-</i>						Cornaceæ					
lobula .....				x		<i>Nyssa sylvatica</i> .....				x	
Osmundaceæ						Ericaceæ					
<i>Osmunda cinnamo-</i>						<i>Clethra acuminata</i> ....				x	x
mea .....		x	x			<i>Monotropa uniflora</i> ..	x		x		
Lycopodiaceæ						<i>Rhododendron maxi-</i>					
<i>Lycopodium com-</i>						mum .....		x		x	
planatum .....					x	<i>R. catawbiense</i> .....	x				
Pinaceæ						<i>R. punctatum</i> .....	x				
<i>Pinus pungens</i> .....					x	<i>Menziesia pilosa</i> .....	x				
<i>Picea rubra</i> .....	x					<i>Dendrium prostratum</i> ..	x				
<i>Abies fraseri</i> .....	x					<i>Kalmia latifolia</i> .....	x		x		
Liliaceæ						<i>Leucothoe catesbæi</i> ..			x		
<i>Trillium undulatum</i> ..	x					<i>Andromeda flori-</i>					
<i>Smilax rotundifolia</i> ..				x	x	bunda .....				x	x
Orchidaceæ						<i>Lyonia ligustrina</i> ..				x	x
<i>Habenaria ciliaris</i> ..				x	x	<i>Oxydendrum arbo-</i>					
Fagaceæ						reum .....				x	x
<i>Castanea dentata</i> .....				x		<i>Epigæa repens</i> .....					x
Magnoliaceæ						<i>Gaultheria procum-</i>					
<i>Magnolia fraseri</i> .....		x	x			bens .....					x
Lauraceæ						<i>Gaylussacia ursina</i> ..				x	
<i>Sassafras variifolium</i> ..				x	x	<i>G. baccata</i> .....					x
Saxifragaceæ						<i>Vaccinium arboreum</i> ..	x				
<i>Saxifraga leucanth-</i>						<i>V. corymbosum</i> .....	x				
mifolia .....	x					<i>V. corymbosum palli-</i>					
<i>Ribes prostratum</i> .....	x					dum .....	x				
Hamamelidaceæ						<i>V. erythrocarpum</i> .....	x				
<i>Hamamelis virginiana</i> ..				x		Diapensiaceæ					
Rosaceæ						<i>Galax aphylla</i> .....				x	x
<i>Pyrus americana</i> .....	x					Gentianaceæ					
<i>P. melanocarpa</i> .....		x				<i>Gentiana linearis</i> .....	x				
<i>Amelanchier canad-</i>						Scrophulariaceæ					
sis .....		x				<i>Melampyrum lineare</i> ..				x	x
<i>Geum peckii</i> .....	x					Caprifoliaceæ					
<i>Rubus canadensis</i> .....	x					<i>Diervilla sessilifolia</i> ..	x				
<i>Prunus pennsylvanica</i> ..	x					<i>Viburnum cassi-</i>					
Leguminosæ						noides .....	x				
<i>Robinia pseudo-aca-</i>						Compositæ					
cia .....				x	x	<i>Solidago glomerata</i> ..	x	x			
Anacardiaceæ											
<i>Rhus copallina</i> .....				x	x						

Summary—54 species are listed in the flora of the balds; 40 species (74 per cent) are shrubs, or, in some cases, scrubby trees; 21 species (39 per cent) of the total flora belong to the Ericales (with one exception, the Ericaceæ of Gray); 19 species of the woody plants (47.5 per cent) belong to the Ericaceæ.

<sup>1</sup>Nomenclature after Gray as far as possible, otherwise after Small.

The main point to be derived in this connection is that the species in the heath balds are for the most part to be found also in the adjacent forests. In other words, they do not have a very great fidelity to the heath bald communities. On the peaks and ridges these shrub species develop an exclusiveness and luxuriance that makes them stand out as islands in the surrounding forests. At the same time, however, the heath balds maintain a similarity in physiognomy despite the changing species content. The relation of the bald species to altitude, which is in reality the relation to the contiguous forest type, is brought out in the following table (II), the columns of which are numbered as follows:

*6,500 Feet, Approximate Altitude*—1, Mt. LeConte, Maintop bald; 2, Mt. LeConte, West Point bald; 3, Mt. LeConte, Balsamtop bald; 4, Mt. LeConte, South Balsamtop bald; 5, Mt. LeConte, East Point bald; 6, Mt. LeConte, Myrtle Point bald.

*5,000 Feet Approximate Altitude*—1, Brushy mountain; 2, Chimney Caps; 3, Mt. LeConte, Beartrap bald; 4, Mt. LeConte, Rocky Spur bald; 5, Mt. LeConte, Alum Cave balds; 6, Walker Prong balds.

*4,000 Feet, Approximate Altitude*—1, Brushy mountain, Taterhill lead bald; 2, Brushy mountain, First lead bald; 3, Brushy mountain, Second lead bald; 4, Ball mountain; 5, Mt. LeConte, Bullhead bald.

In Table II the seventeen balds studied are grouped into three sections according to their approximate altitudes. The woody species are arranged in sequence which approximates their "constancy" in the balds. Braun-Blanquet and Pavillard, in their "Vocabulaire de Sociologie Vegetale" (1), make the following statement about constance: "La CONSTANCE est une expression relative de la Presence, rapportee a des aires-eschantillons de dimensions determinees, mais assez grandes, prelevees une seule fois dans chaque individu d'association. En combinant les resultats des determinations de frequence avec ceux de la Constance, on obtient une expression synthetique de la repartition plus our moins uniforme des especes dans l'ensemble des individus d'association, c'est-a-dire une expression plus ou moins approximative de l'homogeneite de l'association." As a consequence, it is seen that only two species, *Rhododendron catawbiense* and *Vaccinium corymbosum*, are 100 per cent constant in that they occur in all seventeen

TABLE II

WOODY SPECIES	APPROXIMATE ALTITUDE																	
	6,500 Feet						5,000 Feet						4,000 Feet					
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	
Rhododendron catawbiense.....	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Vaccinium corymbosum.....	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Rhododendron punctatum.....	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Dendrium prostratum.....	x	..	x	x	..	x	x	x	x	x	x	x	..	..	..	..	..	..
Vaccinium erythrocarpum.....	x	x	x	x	x	x	..	x	..	..	x	x	..	..	..	..	..	..
Menziesia pilosa.....	x	x	x	..	..	x	..	..	..	..	..	..	..	..	..	..	..	..
Pyrus americana.....	x	x	x	x	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Prunus pennsylvanica.....	x	x	..	..	..	x	..	..	..	..	..	..	..	..	..	..	..	..
Picea rubra.....	x	..	..	x	x	x	..	..	..	..	..	..	..	..	..	..	..	..
Abies fraseri.....	x	..	..	x	x	x	..	..	..	..	..	..	..	..	..	..	..	..
Ribes prostratum.....	..	..	x	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Rubus canadensis.....	..	x	x	..	..	..	..	x	..	x	x	..	..	..	..	x	..	..
Diervilla sessilifolia.....	..	..	x	..	..	..	..	x	..	x	..	..	..	..	..	..	..	..
Kalmia latifolia.....	..	..	..	..	..	..	x	x	x	x	x	x	x	x	x	x	x	x
Pyrus melanocarpa.....	..	..	..	..	x	..	x	..	x	..	x	x	x	..	..	..	x	..
Lyonia ligustrina.....	..	..	..	..	..	..	x	..	..	x	..	..	..	..	..	..	..	x
Gaylussacia baccata.....	..	..	..	..	..	..	x	..	..	..	..	..	..	..	..	..	..	x
Nyssa sylvatica.....	..	..	..	..	..	..	x	..	..	..	..	..	..	..	..	..	..	x
Ilex monticola.....	..	..	..	..	..	..	..	x	x	x	..	x	x	x	x	x	x	x
Clethra acuminata.....	..	..	..	..	..	..	x	..	x	..	x	x	x	x	x	x	x	x
Viburnum cassinoides.....	..	..	..	..	..	..	x	..	x	..	x	x	..	x	..	x	x	x
Smilax rotundifolia.....	..	..	..	..	..	..	x	..	..	..	..	..	x	x	x	x	x	x
Acer rubrum.....	..	..	..	..	..	..	x	..	x	..	x	..	..	x	x	x	x	x
Robinia pseudo-acacia.....	..	..	..	..	..	..	..	..	x	..	..	..	..	..	..	..	..	x
Andromeda floribunda.....	..	..	..	..	..	..	..	..	..	x	x	..	..	..	..	..	x	x
Amelanchier canadensis.....	..	..	..	..	..	..	x	..	x	..	..	..	..	x	x	x	x	x
Rhododendron maximum.....	..	..	..	..	..	..	x	..	..	..	..	..	x	x	x	x	x	x
Leucothoe catesbaei.....	..	..	..	..	..	..	x	..	..	..	..	..	x	x	..	..	..	..
Oxydendrum arboreum.....	..	..	..	..	..	..	x	..	..	..	..	..	..	..	..	x	x	..
Pinus pungens.....	..	..	..	..	..	..	..	..	..	..	..	x	..	x	x	..	x	..
Sassafras variifolium.....	..	..	..	..	..	..	..	..	..	..	..	..	..	x	..	..	x	..
Gaylussacia ursina.....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	x
Gastanea dentata.....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	x
Hamamelis virginiana.....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	x
Number of species in each bald.....	10	8	10	8	7	9	16	7	12	10	12	11	10	14	12	14	22	
Average number of species.....	9						11						14					

examples of the heath bald association. *Kalmia latifolia* is found to be present in all examples of the heath balds at the two lower levels.

The three altitudinal groups are more or less natural and distinguishable on a basis of their species. The highest group of balds, however, is more sharply distinguished than those at 5,000 and 4,000 feet elevation. The group at the highest altitude can be said to be distinguished by the presence of species from the adjacent spruce-fir forests, as *Menziesia pilosa*, *Pyrus americana*, *Prunus pennsylvanica*, *Ribes prostratum* and *Abies fraseri* and *Picea rubra*. The group at 5,000 feet altitude

can be distinguished by the presence of *Rhododendron punctatum* and *Dendrium prostratum*, in addition to *Kalmia latifolia*, which is usually one of the dominants. The lower group of balds also has *Kalmia latifolia* as one of the dominants, but *Rhododendron punctatum* and *Dendrium prostratum* are missing.

There are other characteristics which help to distinguish the various aspects of the heath balds, such as degree of raw peat formation, presence of *Sphagnum*, etc., which will be taken up elsewhere.

The relatively greater importance of certain species in the various examples of the heath bald is indicated in the tabulation by the bold-face "x." They may be considered as the "dominants," although the conclusion is based in most of the cases upon observation without the aid of statistical procedure. Certain of the species deserve special comment. For example, the presence of *Abies* and *Picea* in the heath balds is without successional significance in most, if not all cases. Occasional seedlings are able to establish and grow for a number of years, in fact, sometimes until their tops exceed the height of the shrub vegetation, at which time they are very quickly top-killed, if not completely eliminated. In fact, very few seedlings are able to establish in the heath balds in the first place. The random appearance of certain tree species at lower elevations might also be misleading, as *Robinia pseudo-acacia*, *Oxydendrum arboreum*, *Pinus pungens*, *Castanea dentata* and *Hamelis virginiana*. They are of insufficient importance, however, to indicate the replacement of heath bald associations by trees, except possibly in the case of Bullhead bald. At the present it can be said that the heath balds, at both low and high altitudes, are probably derived from forested types by the elimination of the trees and that they are maintaining themselves as treeless areas of the broad-sclerophyll-scrub type. In other words, they are post-climax "islands" in the contiguous coniferous and broad-leaf formations. This matter is to be considered in more detail elsewhere.

#### STATISTICAL STUDIES: LIFE-FORM CLASSES

The use of life-form concepts in plant geography has received a great impetus since the introduction of Raunkiaer's life-form classes and biological spectrum. When the flora of a region of sufficient size, or of a formation or association, is classified according to Raunkiaer's standard groups and percentages are determined, there results a "spectrum"

which can be compared with the normal spectrum, a more or less arbitrary standard. Deviations from the arbitrary "normal" in the major groups characterize climatic formations, while minor differences within types of vegetation, for example the temperate deciduous forest, are also discernable.

In his 1908 paper (see Smith 18), Raunkiaer used the following classes based on the degree of protection afforded the perennating bud:

- I. Phanerophytes (woody plants): (MM) Meso- and Megaphanerophytes (from 8 to 30 meters and over 30 meters in height); (M) Microphanerophytes (from 2 to 8 meters in height); (N) Nanophanerophytes (from 25 cm to 2 meters high).
- II. (Ch) Chamæphytes (creeping or rosette plants with the perennating buds on the surface or not more than 25 cm above the soil).
- III. (H) Hemicryptophytes (herbaceous, with dormant buds in the surface of the ground).
- IV. Cryptophytes: (G) Geophytes (buds subterranean); (HH) Helophytes and Hydrophytes (aquatic species with buds in the muck or water).
- V. (Th) Therophytes (annuals: buds in the seed).
- VI. (E) Epiphytes.
- VII. (S) Stem Succulents.

Raunkiaer's normal spectrum contains the following percentages for each class:

MM	M	N	Ch	H	G	HH	Th	E	S
6	17	20	9	27	3	1	13	3	1

Illustrations of the use of life-form classes could be added but are not necessary, since it is quite generally recognized that the type of spectrum of a region is an indication of the climatic conditions. To quote from Miss Ennis (6), who has done the best piece of work in America along this line: "The life-forms of the plants in the flora of a region present a definite response to the climate of that region."

The following table and summary (Table III) present the flora of the heath balds of the Great Smoky mountains according to their life-form classes. The most conspicuous feature is the high percentage of phanerophytes of two classes, namely, nanophanerophytes, 22.2 per cent, and microphanerophytes, 48.1 per cent, making a total of 70 per cent, as against 37 per cent in the normal spectrum for the same height

TABLE III

## LIFE-FORM CLASSES OF THE HEATH BALD FLORA

FLORA	Life-form Classes						FLORA	Life-form Classes					
	M	N	Ch	H	G	Th		M	N	Ch	H	G	Th
<i>Pteris aquilina</i> .....					X		<i>Nyssa sylvatica</i> .....						
<i>Aspidium spinulosum</i> inter- medium.....				X			<i>Clethra acuminata</i> .....	X	X				
<i>Dicksonia punctilobula</i> .....				X			<i>Monotropa uniflora</i> .....				X		
<i>Osmunda cinnamomea</i> .....				X			<i>Rhododendron maximum</i> .....	X	X				
<i>Lycopodium complanatum</i> .....				X			<i>R. catawbiense</i> .....	X	X				
<i>Pinus pungens</i> .....	X						<i>R. punctatum</i> .....		X				
<i>Picea rubra</i> .....	X	X					<i>Menziesia pilosa</i> .....		X				
<i>Abies fraseri</i> .....	X	X					<i>Dendrium prostratum</i> .....		X				
<i>Trillium undulatum</i> .....				X			<i>Kalmia latifolia</i> .....	X	X				
<i>Smilax rotundifolia</i> .....	X	X					<i>Leucothoe catesbaei</i> .....		X				
<i>Habenaria ciliaris</i> .....				X			<i>Andromeda floribunda</i> .....	X	X				
<i>Castanea dentata</i> .....	X	X					<i>Lyonia ligustrina</i> .....		X				
<i>Magnolia fraseri</i> .....	X	X					<i>Oxydendrum arboreum</i> .....	X	X				
<i>Sassafras variifolium</i> .....	X	X					<i>Epigaea repens</i> .....			X			
<i>Saxifraga leucanthemifolia</i> .....				X			<i>Gaultheria procumbens</i> .....			X			
<i>Ribes prostratum</i> .....		X					<i>Gaylussacia ursina</i> .....		X				
<i>Hamamelis virginiana</i> .....	X	X					<i>G. baccata</i> .....		X				
<i>Pyrus americana</i> .....	X	X					<i>Vaccinium arboreum</i> .....	X	X				
<i>P. melanocarpa</i> .....	X	X					<i>V. corymbosum</i> .....	X	X				
<i>Amelanchier canadensis</i> .....	X	X					<i>V. corymbosum pallidum</i> .....	X	X				
<i>Geum peckii</i> .....				X			<i>V. erythrocarpum</i> .....		X				
<i>Rubus canadensis</i> .....		X					<i>Galax aphylla</i> .....			X			
<i>Prunus pennsylvanica</i> .....	X	X					<i>Gentiana linearis</i> .....			X			
<i>Robinia pseudo-acacia</i> .....	X	X					<i>Melampyrum lineare</i> .....					X	
<i>Rhus copallina</i> .....	X	X					<i>Diervilla sessilifolia</i> .....		X				
<i>Ilex monticola</i> .....	X	X					<i>Viburnum cassinoides</i> .....	X	X				
<i>Acer rubrum</i> .....	X	X					<i>Solidago glomerata</i> .....			X			

## TABULATION

LIFE-FORM CLASSES	No. Species	PER CENT	
		Heath Bald	Normal Spectrum
Phanerophytes			
Microphanerophyte (M).....	26	48.1	17
Nanophanerophyte (N).....	12	22.2	70.4
Chamaephyte (Ch).....	2	3.7	9
Hemicryptophyte (H).....	8	14.8	27
Cryptophyte			
Geophyte (G).....	5	9.2	3
Therophytes (Th).....	1	1.9	13
	54	99.9	—

classes of phanerophytes. Therophytes are conspicuously low in number, while the other classes are also low or absent in sufficient extent to account for the excess of low-growing phanerophytes. Many of the microphanerophytes fall into the nanophanerophyte class, if considered only from the lower altitudes.

## STATISTICAL STUDIES: LEAF-SIZE CLASSES

As Fuller and Bakke (9) point out, "Ecology is one of the most difficult branches of botany when one attempts to measure or estimate with exactness the value of a single character and thus determine its significance, not from any specific peculiarity but because it embraces all the relations and the difficulties of botany taken as a whole." Thus it must be considered an important advance that plant geographers and ecologists have attempted statistical methods of vegetation analysis. In a comparison of different types of vegetation, one of the conspicuous variables, relatively easy to measure, is leaf size. Raunkiaer has selected, as a result of considering a large number of species, six leaf-size classes, which he maintains are more or less natural. The use of these leaf-size classes enables a more accurate description than words alone could convey in an analysis of a piece of vegetation. The limits of the six classes are set as follows:

1. Leptophyll (Le), 25 sq. mm. or less. 2. Nanophyll (Na),  $9 \times 25$  sq. mm.—equals 225 sq. mm. 3. Microphyll (Mi),  $9^2 \times 25$  sq. mm.—equals 2,025 sq. mm. 4. Mesophyll (Me),  $9^3 \times 25$  sq. mm.—equals 18,225 sq. mm. 5. Macrophyll (Ma),  $9^4 \times 25$  sq. mm.—equals 164,025 sq. mm. 6. Megaphyll (Mg), larger than macrophyll.

Scale drawings of these leaf-size classes are to be found in the paper by Fuller and Bakke (9) and can be used in determining the proper leaf-size class of any species, and is of considerable utility, since the above figures, in the abstract, do not convey any idea of the actual size.

The first step in leaf-size classification involves separation of the species on the following bases, after which the percentages of each leaf-size class are computed for each group. Group 1—Deciduous: species with simple and lobed leaves. Group 2—Deciduous: species with lacerated and decompound leaves. Group 3—Evergreen species. Group 4—Aphyllous species.

The following table and summary present (Table IV) the data for the complete heath bald flora according to the system described. In addition those that are woody species are indicated.

The table of leaf-size classes is sufficiently clear and detailed to obviate any lengthy discussion of the factors involved. Eight species are ericaceous, falling into the following description, *evergreen-broad-leaved-microphylls*, which includes the dominants of the flora except

TABLE IV

FLORA	Aphyl- lous	Conif- erous	EVERGREEN				Me	DECIDUOUS								Woody	
			Le	Na	Broad Mi	Le		Na	Simple Mi	Me	Ma	Le	Pinnate Na	Mi			
<i>Pteris aquilina</i> .....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	X	..	..
<i>Aspidium spinulosum in- termedium</i> .....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	X	..	..
<i>Dicksonia punctilobula</i> ..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	X	..	..
<i>Osmunda cinnamomea</i> ....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	X	..	..
<i>Lycopodium complana- tum</i> .....	..	X*	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
<i>Pinus pungens</i> .....	..	X	..	..	..	..	..	..	..	..	..	..	..	..	..	..	X
<i>Picea rubra</i> .....	..	X	..	..	..	..	..	..	..	..	..	..	..	..	..	..	X
<i>Abies fraseri</i> .....	..	X	..	..	..	..	..	..	..	..	..	..	..	..	..	..	X
<i>Trillium undulatum</i> .....	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	..
<i>Smilax rotundifolia</i> .....	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	X
<i>Habenaria ciliaris</i> .....	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	..
<i>Castanea dentata</i> .....	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	X
<i>Magnolia fraseri</i> .....	..	..	..	..	..	..	..	..	..	..	..	X	..	..	..	..	X
<i>Sassafras variifolium</i> ....	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	X
<i>Saxifraga leucanthemi- folia</i> .....	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	..
<i>Ribes prostratum</i> .....	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	X
<i>Hamamelis virginiana</i> ...	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	X
<i>Pyrus americana</i> .....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	X	X	..
<i>P. melanocarpa</i> .....	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	X
<i>Amelanchier canadensis</i> ..	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	X
<i>Geum peckii</i> .....	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	..
<i>Rubus canadensis</i> .....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	X	X	..
<i>Prunus pennsylvanica</i> ....	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	X
<i>Robinia pseudo-acacia</i> ...	..	..	..	..	..	..	..	..	..	..	..	..	..	X	..	..	X
<i>Rhus copallina</i> .....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	X	X	..
<i>Ilex monticola</i> .....	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	X
<i>Acer rubrum</i> .....	..	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	X
<i>Nyssa sylvatica</i> .....	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	X
<i>Clethra acuminata</i> .....	..	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	X
<i>Monotropa uniflora</i> .....	X	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
<i>Rhododendron maxi- mum</i> .....	..	..	..	..	..	X	..	..	..	..	..	..	..	..	..	..	X
<i>R. catawbiense</i> .....	..	..	..	..	X	..	..	..	..	..	..	..	..	..	..	..	X
<i>R. punctatum</i> .....	..	..	..	..	X	..	..	..	..	..	..	..	..	..	..	..	X
<i>Menziesia pilosa</i> .....	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	..	X
<i>Dendrium prostratum</i> ....	..	X	..	..	..	..	..	..	..	..	..	..	..	..	..	..	X
<i>Kalmia latifolia</i> .....	..	..	..	..	X	..	..	..	..	..	..	..	..	..	..	..	X
<i>Leucothœ catesæi</i> .....	..	..	..	..	X	..	..	..	..	..	..	..	..	..	..	..	X
<i>Andromeda floribunda</i> ...	..	..	..	..	X	..	..	..	..	..	..	..	..	..	..	..	X
<i>Lyonia ligustrina</i> .....	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	X
<i>Oxydendrum arboreum</i> ...	..	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	X
<i>Epigæa repens</i> .....	..	..	..	..	X	..	..	..	..	..	..	..	..	..	..	..	X
<i>Gaultheria procumbens</i> ..	..	..	..	..	X	..	..	..	..	..	..	..	..	..	..	..	X
<i>Gaylussacia ursina</i> .....	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	X
<i>G. baccata</i> .....	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	..	X
<i>Vaccinium arboreum</i> ....	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	X
<i>V. corymbosum</i> .....	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	X
<i>V. corymbosum palli- dum</i> .....	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	X
<i>V. erythrocarpum</i> .....	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	X

FLORA	Aphyllous	Coniferous	EVERGREEN				Le	Na	DECIDUOUS				Le	Na	Mi	Woody
			Le	Na	Broad	Me			Simple	Me	Ma	Pinnate				
Galax aphylla.....	..	..	..	..	X	..	..	..	..	..	..	..	..	..	..	..
Gentiana linearis.....	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	..
Melampyrum lineare.....	..	..	..	..	..	..	..	X	..	..	..	..	..	..	..	..
Diervilla sessilifolia.....	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	X
Viburnum cassinoides.....	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	X
Solidago glomerata.....	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	..

TABLE V

## SUMMARY OF LEAF-SIZE CLASS DATA

CLASSIFICATION	TOTAL FLORA		WOODY FLORA		ERICALES	
	No. Sp.	Per Cent	No.	Per Cent	No. Species	Dominants
APHYLLOUS .....	1	2	..	..	1	..
EVERGREEN .....	14	26	12	30	10	5
Scale-leaved .....	1	..	..	..	..	..
Needle-leaved .....	3	..	3	..	..	..
Broad-leaved .....	10	19	9	23	10	5
Leptophyll .....	1	..	1	..	..	1
Nanophyll .....	0	..	..	..	..	..
Microphyll .....	8	15	7	18	8	3
Mesophyll .....	1	..	1	..	1	1
DECIDUOUS .....	39	72	28	70	10	1
Simple .....	31	57	24	60	10	1
Leptophyll .....	0	..	..	..	..	..
Nanophyll .....	3	..	2	..	2	..
Microphyll .....	22	41	17	42	6	1
Mesophyll .....	5	..	4	..	2	..
Macrophyll .....	1	..	1	..	..	..
Pinnately compound .....	8	15	4	10	..	..
Leptophyll .....	2	..	..	..	..	..
Nanophyll .....	3	..	1	..	..	..
Microphyll .....	3	..	3	..	..	..
Woody species.....	40	74	40	..	20	..
Herbaceous .....	14	26	..	..	1	..

for *Vaccinium*. Such a physiognomy has been described as "broad-sclerophyll scrub" by Cooper (4). This form is fairly common in two types of situations: mild temperate districts with winter rain and prolonged summer drought, and cool humid regions. In respect to the first type of situation, the regions which possess such a climate and support such a vegetation are, according to Schimper (17), the Mediterranean shores, the southwest extremity of Africa, southwestern and much of southern Australia, central Chile and California. The second type develops in regions of high humidity, where even in summer heavy mists arise daily or almost daily. . . . The leaves belong to the laurel-form, that is to say, they are undivided, entire and coriaceous. To

the latter the heath-scrub communities of the Great Smoky mountains must be assigned.

Since most of the species characteristic of the heath balds are found also in the contiguous forests, it is important to bring out the fact that the open nature and exposure of the bald situations result in a considerable change of leaf-size, when the heath bald is contrasted with the spruce-fir forest, for identical species. This is brought out in the following table (VI), where the average size, and maximum ranges are presented for 100 representative leaves of each of seven species. Half of the leaves were taken from bald situations and half from nearby plants growing under the protection of the forest. The leaves for *Rhododendron maximum*, *Kalmia latifolia* and *Lyonia ligustrina* are from the bald on Brushy mountain at approximately 5,000 feet elevation. The remaining species are from the balds on Mt. LeConte at an elevation of about 6,500 feet. In each instance the more mesophytic forms are from close by, at somewhat lower elevations.

In addition to a decrease in the average size of the leaf blades, there are other changes of xeromorphic character: (1) leaf margins are revolute (sometimes *Rhododendron catawbiense* leaves are incurled until their margins meet); (2) leaves are likely to be more hairy or scurfy than under the trees; color is darker, and (4) the petioles and branches are stouter and shorter.

The following table gives the data as to dimensions. The average length and width of a leaf is frequently about half in the balds of that in the forest. In the instance of *Rhododendron catawbiense* and *Menziesia pilosa*, the difference is such as to change the species from one leaf-size class to the next one smaller.

## STATISTICAL STUDIES: QUADRAT STUDIES

Brushy mountain heath bald, 5,000 feet elevation, was selected for quadrat studies because of its extensive development and intermediate altitudinal position. Kenoyer (11) has made a study of Raunkiaer's so-called "Law of Frequency" on American vegetation and found the principle sound. The main differences between Raunkiaer's and Kenoyer's ratios of frequency classes seem to be a result of American plant associations being generally richer in species. Translating Braun-Blanquet and Pavillard (1) we have the following definition of frequency:

TABLE VI

COMPARISON OF LEAF SIZES (BLADES) OF SOME ERICADS GROWN IN  
HEATH BALDS AND UNDER PROTECTION OF FOREST

(Each measurement is based on 50 representative leaves.)

NAME OF PLANT	Length in cm.		Width in cm.	
	Mesophyte Woodland	Xerophyte Bald	Mesophyte Woodland	Xerophyte Bald
<i>Rhododendron maximum</i> (Mesophyll)				
Largest dimension.....	26.4	16.2	8.6	5.4
Smallest dimension.....	15.1	6.8	4.9	2.2
Average dimension.....	20.71	11.38	6.69	3.58
<i>Rhododendron catawbiense</i> (Microphyll and Mesophyll)				
Largest dimension.....	18.5	10.5	7.1	4.3
Smallest dimension.....	8.1	3.6	3.7	1.5
Average dimension.....	13.53	6.90	5.90	2.97
<i>Rhododendron punctatum</i> (Microphyll)				
Largest dimension.....	11.2	6.9	3.9	3.3
Smallest dimension.....	4.0	2.5	1.2	1.0
Average dimension.....	8.21	4.20	2.81	1.80
<i>Menziesia pilosa</i> (Nanophyll and Microphyll)				
Largest dimension.....	6.7	3.1	2.8	1.7
Smallest dimension.....	1.5	1.2	0.7	0.6
Average dimension.....	4.34	2.03	1.91	1.52
<i>Vaccinium erythrocarpum</i> (Microphyll)				
Largest dimension.....	7.5	6.3	2.7	2.5
Smallest dimension.....	1.6	0.8	1.5	0.6
Average dimension.....	5.34	4.01	1.86	1.68
<i>Kalmia latifolia</i> (Microphyll)				
Largest dimension.....	10.5	4.8	4.1	2.2
Smallest dimension.....	2.9	1.6	1.2	0.6
Average dimension.....	7.26	3.60	3.03	1.47
<i>Lyonia ligustrina</i> (Microphyll)				
Largest dimension.....	6.9	5.7	3.7	3.8
Smallest dimension.....	3.0	2.8	1.6	1.0
Average dimension.....	5.16	4.07	2.85	2.13

"Frequency is a statistical expression derived by preparing complete floristic lists of a certain number of sample areas (quadrats) of equal dimension, disseminated as much as possible throughout the extent of the individual example of the association." The information so derived is usually handled as follows: the frequency of a species in an association is the relation expressed in per cent between the number of quadrats which contained it and the total number of quadrats analyzed in the particular association. As a matter of convenience, the percentages

are usually divided into five classes, as follows: Class A, species with 1-20 per cent frequency; Class B, species with 21-40 per cent frequency; Class C, species with 41-60 per cent frequency; Class D, species with 61-80 per cent frequency; Class E, species with 81-100 per cent frequency.

It will then be found that a certain percentage of the total number of species encountered in the association will fall into Class A, Class B, etc., with Class A greater than B, B larger than C, C larger than D, but with E larger than D, as follows:  $A > B > C > D < E$ .

Raunkiaer and Kenoyer found numerical values for the classes as follows:

TABLE VII

AUTHOR	Vegetation and No. of Percentages Involved	Per Cent. in Frequency Classes				
		A	B	C	D	E
Raunkiaer	European 8,087%	53	14	9	8	16
Kenoyer	American 1,425%	69	12	6	4	9

Furthermore, Kenoyer (11) established the valuable fact that twenty-five quadrats of sufficient size, widely distributed in an homogeneous association, are sufficient for a statistical analysis of frequency. Romell (16) emphasizes that "statistics made with different sizes of sample areas cannot be compared." The commonest quadrat sizes are 0.1 m, 1 m, and 10 m on a side. In studying various associations in the Great Smoky mountains, 1-meter quadrats have been used exclusively. The results of two series of twenty-five quadrats are expressed in the following tables (VIII and IX).

The presence of a species in a quadrat is indicated by a number which stands for the coverage class of the species, and is termed "dominance" by Braun-Blanquet and Pavillard. They say: "Dominance concerns the extent, volume and surface, occupied or covered by the individuals of each species." In many-layered groups it must be evaluated separately for each stratum. As in the case of frequency, five classes are used in expressing degree of dominance. Class 1—1-5 per cent coverage; Class 2—6-25 per cent coverage; Class 3—26-50 per cent coverage; Class 4—51-75 per cent coverage; Class 5—76-100 per cent coverage.

When several species are present in one quadrat and dominance figures (classes) are given each which total more than 5, it is to be under-

TABLE VIII

## BRUSHY MOUNTAIN HEATH BALD—IN AREA OF FIRST AND SECOND BURN, 1929

SPECIES	25 Quadrats: Numbers = Coverage																									
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25 Pct.	
<i>Acer rubrum</i> .....	..	..	..	..	..	..	..	..	..	..	..	..	2	..	..	..	..	..	..	..	..	..	..	..	4	
<i>Amelanchier canadensis</i> .....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2	..	..	..	..	..	..	..	..	4	
<i>Clethra acuminata</i> .....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	4	
<i>Dendrium prostratum</i> .....	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	1	..	12	
<i>Galax aphylla</i> .....	1	1	1	..	2	..	..	..	..	..	..	1	..	..	..	..	..	1	..	1	..	1	..	..	32	
<i>Gaultheria procumbens</i> .....	..	5	1	2	..	..	1	1	1	..	2	..	1	1	..	..	..	..	..	..	..	1	..	..	40	
<i>Gaylussacia baccata</i> .....	2	..	3	..	2	3	..	..	..	..	..	..	..	..	1	..	..	3	..	3	..	1	..	..	32	
<i>Ilex monticola</i> .....	..	..	..	..	..	..	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	4	
<i>Kalmia latifolia</i> .....	2	1	3	3	2	3	4	1	1	2	1	2	..	..	..	..	3	1	2	1	1	2	1	4	2	88
<i>Lyonia ligustrina</i> .....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	2	..	..	..	4	
<i>Osmunda cinnamomea</i> .....	..	..	..	..	..	..	..	..	..	..	..	..	5	..	..	..	..	..	..	..	..	..	..	..	4	
<i>Picea rubra</i> (Top dead).....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	4	
<i>Pteris aquilina</i> .....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	4	
<i>Pyrus melanocarpa</i> .....	..	..	..	..	..	..	..	..	..	..	..	3	..	1	..	..	..	..	2	..	..	..	..	..	12	
<i>Rhododendron catawbiense</i> .....	1	1	2	1	4	2	1	1	5	2	4	..	..	3	2	1	3	2	2	..	2	..	4	1	3	84
<i>Smilax rotundifolia</i> .....	..	..	..	..	..	..	..	1	..	..	..	..	..	..	1	..	..	..	1	..	..	..	..	..	12	
<i>Vaccinium corymbosum</i> (?).....	..	..	1	..	..	2	1	..	..	1	..	..	..	2	3	3	1	..	2	..	1	..	1	..	44	
<i>Viburnum cassinoides</i> .....	1	..	1	..	..	1	..	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	16	
Number of species (18).....	5	5	5	3	4	6	4	3	4	3	4	2	5	5	4	3	4	4	4	5	4	2	4	4	...	

Frequency Classes A &gt; B &gt; C &gt; D &lt; E = 67-17-5-0-11

TABLE IX

BRUSHY MOUNTAIN HEATH BALD—IN AREA OF MOST RECENT BURN, TAKEN 1930

SPECIES	25 Quadrats: Numbers = Coverage																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25 Pct.
<i>Clethra acuminata</i> .....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	4
<i>Dendrium prostratum</i> .....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	1	..	..	..	1
<i>Epigaea repens</i> .....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	3	1	..	..	..	..	..	..	..	8
<i>Galax aphylla</i> .....	..	..	..	2	..	..	..	2	2	2	2	2	..	..	..	2	2	..	..	1	1	1	..	1	52
<i>Gaultheria procumbens</i> .....	4	1	4	2	2	2	3	4	1	2	3	3	5	4	2	2	2	1	1	..	2	3	2	2	96
<i>Gaylussacia baccata</i> .....	2	1	4	1	2	3	2	1	..	2	4	2	2	2	3	2	3	2	4	2	2	3	3	2	92
<i>Kalmia latifolia</i> .....	3	2	..	2	2	2	3	4	3	4	3	2	2	5	3	..	3	..	4	..	2	2	1	3	84
<i>Lycopodium obscurum</i> .....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	4
<i>Lyonia ligustrina</i> .....	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	4
<i>Medeola virginiana</i> .....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	4
<i>Melampyrum lineare</i> .....	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	1	..	..	2	..	..	2	..	1	20
<i>Pteris aquilina</i> .....	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2	..	..	4
<i>Pyrus melanocarpa</i> .....	1	1	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	2	2	1	..	28
<i>Rhododendron catawbiense</i> .....	1	4	3	5	1	..	..	1	3	..	..	2	..	..	2	1	..	1	1	2	..	..	..	..	52
<i>Smilax rotundifolia</i> .....	..	1	..	1	..	1	1	1	1	1	1	1	..	2	1	..	1	..	..	..	..	..	..	..	36
<i>Vaccinium corymbosum (P)</i> .....	3	2	1	..	2	..	2	..	..	..	..	..	..	..	2	3	1	..	2	..	..	..	..	..	1
Number of species (16).....	7	6	5	5	4	5	3	5	5	3	5	5	6	4	3	7	8	4	6	8	5	4	6	4	10

Frequency Classes A &gt; B &gt; C &gt; D &lt; E = 50-19-12-0-19

stood that lower shrubs or herbs, like *Dendrium*, *Galax*, *Gaultheria*, etc., are underneath *Kalmia*, *Vaccinium* and *Rhododendron*, and thus have overlapping coverage. The twenty-five quadrats analyzed in 1930 in the area of the most recent burn (several years ago), indicate a relative importance of *Gaylussacia baccata* and *Gaultheria procumbens* 92 per cent and 96 per cent frequency, which has dropped off in the areas of the older burns, where they enjoy frequency of 32 and 40, respectively. *Kalmia latifolia* and *Rhododendron catawbiense* have about the same frequency in both areas. These species are to be considered most important in the association on Brushy mountain.

## FACTORS IN INITIATION, MAINTENANCE AND DISTRIBUTION OF HEATH BALDS

CLIMATIC FACTORS.—In the absence of quantitative weather data in the vicinity of the Great Smoky mountains, one has to depend on fragmentary field data and general observations. In the region of the heath balds the climate can be briefly described as "oceanic" despite the inland location. Rainfall and relative humidity are high, while the temperature tends to be low, but subject to fluctuations. Evaporation, as measured by the Livingston atmometers, is generally quite low.

Rainfall in the higher regions is said to exceed 80 inches a year, a contention well substantiated by a comparison of the vegetation of the Smoky mountains with regions of high rainfall in North Carolina where records have been kept: at Mt. Mitchell near Asheville, and in the southern Blue Ridge mountains at Highlands, North Carolina. In respect to the humidity, it is apparent that the development of heath balds is closely related to upper altitudes almost constantly enveloped by clouds, especially during summer months.

Temperatures are generally low and equable (see Table XIII), yet 90 degrees Fahrenheit was frequently reached in the abnormal summer of 1930. The winters may frequently have short periods as cold as 18 degrees below zero, as in December, 1928. It is in the winter periods, with frost, sleet, high winds and sudden and extreme drops in temperature, that the exposed situations of the heath balds, which are generally without the protection of deep snow, present the greatest demands on the heath bald species. Otto Stocker (20 and 21), dealing with the problem of xeromorphy of heath and bog plants, proposes that they should be considered as "anemorphs," since, as he says, "the leaf structure of

the Ericaceæ seems to be an adaptation to the very heavy winter storms of heath and bog regions rather than to decreased transpiration."

In the summer the climatic conditions in the Great Smoky mountains do not seem to be particularly important in the maintenance of the heath balds. In this connection, see the following evaporation rates from Livingston (12) atmometers for midsummer periods in 1928 and 1929, Tables X and XI. Station A was located in what seemed to be a representative situation in Maintop heath bald, Mt. LeConte. The spruce-fir station, C, was in a pole stand north of the spring about one-fourth mile distant from A but at almost the same elevation. In this sort of place the ericads are relatively unimportant. Station B was considered transitional because of the heavy development of ericads under the fir. Atmometers were maintained in pairs at all stations and were frequently checked for working order, especially as to the Thome rain valves, which were, of course, absolutely necessary in such a rainy region. The 1928 data represent evaporation rates for a "wet" season, while the 1929 records are probably more nearly average. Since the evaporating power of the air is so very low, we may well be curious as to the availability of water to the plant. Stocker (20 and 21), Thatcher (22) and others have shown the transpiration rates of heath and moor plants place them more nearly with mesophytes than with xerophytes, and that the peat substratum cannot be considered "physiologically dry." A recent discussion and summarization of work along this line is to be found in Maximov's (15) recent book on the relation of the plant to water.

TABLE X

WEEKLY EVAPORATION (LIVINGSTON ATMOMETERS) MT. LECONTE,  
ALTITUDE 6,500 FEET

Date, 1928 Week Ending	Heath Bald A	Transition B	Spruce-Fir C
7-7 .....	60.5 cc	39 cc	15 cc
7-14 .....	11	4.5	3
7-21 .....	33	11	8
7-28 .....	22	6	2
8-4 .....	40.5	25.5	7.5
8-11 .....	20	8	4
8-23* .....	27	9.5	4.5
9-5* .....	35.5	9.5	4.5
9-12 .....	62.5	41.5	17
Average, by weekly periods.....	34.6 cc	16.3 cc	7.3 cc

\*Figures given on a seven-day basis.

TABLE XI  
WEEKLY EVAPORATION (LIVINGSTON ATMOMETERS)

Date, 1929 Week Ending	Mt. LeConte, 6,600 Ft.			Brushy Mt., 5,000 Ft.	
	Heath Bald A	Transi- tion B	Spruce- fir C	Beech Gap D	Heath Bald E
8-20 .....	104 cc	30 cc	16 cc	36 cc	95 cc
8-27 .....	117	31	18	41	106
9- 3 .....	61	18	11	23	65
9-10 .....	43	15	9	20	52
9-17 .....	73	29	14	35	87
9-24 .....	93	35	17	38	96
Average weekly amount.....	82 cc	26 cc	14 cc	32 cc	83 cc

The following study, using *Rhododendron catawbiense*, reveals a more rapid transpiration rate on the part of the more "xeromorphic" leaves of plants growing in a peat substratum in a heath bald than by those growing close by, but under the protection of spruce-fir with little or no peat. On Maintop, Mt. LeConte, at an elevation of approximately 6,600 feet, two plants of *Rhododendron catawbiense* were selected for transpiration studies by the cobalt chloride method. Livingston clips (13) with standard color comparisons were used and the length of time required for the change from one color standard to another, on the part of the cobalt chloride paper, was taken to be an inverse measure of the transpiration rates.

One plant used in the study was located at the top of the Maintop heath bald, while the other was just over the crest not more than fifty feet away, but under the protection of the spruce-fir association (here mostly *Abies fraseri*, an endemic). Each leaf studied was about two feet above the ground and was the terminal one of the shoot. Each shoot bore about ten leaves. The two were as nearly comparable as possible. The plant in the bald showed the effect of the association and the environment in many respects: it was short (about four feet high), compact, with the leaves very much reduced and incurled.

The readings were made between three and four in the afternoon, August 9. The results are indicated in Table XII. The four readings for each leaf were made in the same spot, halfway between the midvein and the margin, near the middle of the leaf.

This single set of figures does not warrant any conclusion, yet it is in accord with the extensive observations of Thatcher (22) that heath plants growing in peat are capable of maintaining a high rate of transpiration when compared with soil and that the so-called xerophytic

TABLE XII

## COMPARATIVE TRANSPIRATION RATES OF RHODODENDRON CATAWBIENSE

STATION	Air Temperature Near Leaf	Time for Change of Cobalt Paper	Time of Day
Heath bald.....	28 c	60 seconds	3:00 P. M.
	24.5 c	65 seconds	3:10 P. M.
	24 c	70 seconds	3:15 P. M.
	23 c	130 seconds	3:20 P. M.
Average .....		81 seconds	
Spruce-fir .....	22 c	240 seconds	3:35 P. M.
	21.5 c	225 seconds	3:40 P. M.
	21 c	275 seconds	3:45 P. M.
	20.5 c	320 seconds	3:55 P. M.
Average .....		285 seconds	

leaf structures do not necessarily reduce water loss on a unit area basis. The leaves of *Rhododendron catawbiense* grown in the heath bald are conspicuously smaller, thicker and incurled, *i. e.*, xeromorphic.

The two studies (Table XIII) on diurnal temperature ranges of soil and air in heath bald and spruce-fir show a good contrast in seasons. The 1928 season was cool, rainy and more nearly normal than the excessively warm and dry 1930 season. Each season is well illustrated by the days selected in August. Air temperatures increase and diminish more rapidly than soil temperatures and reach a higher maximum, except in the case of bare sand soil in the heath bald. The soil temperatures in all cases were taken by standard Tycos soil thermometers inserted in the surface peat (except A2, which was in sand) and undisturbed throughout the day. Air temperatures were derived from ordinary thermometers suspended about one foot above the soil. Each station was carefully selected so as to be representative of the vegetation. Consequently, it is seen that the spruce-fir association is very cool in midsummer and almost free from diurnal fluctuations either in air or soil temperatures. The conditions in the heath bald are much more variable, yet are not extreme, soil temperatures being remarkably low where there is a peat layer—and that is characteristic.

EDAPHIC FACTORS.—Since, with the exception of severe winter periods, climatic factors are not directly important in the formation of heath balds (note important secondary effects, however), we may well turn to a consideration of edaphic factors for further elucidation of the heath bald problem.

Upper south-facing slopes are frequently so consistently occupied

TABLE XIII

## AIR AND SOIL TEMPERATURES IN HEATH BALD AND SPRUCE-FIR

	Air Temperature			Soil Temperature			
	Heath. Bald A	Transi- tion B	Spruce- fir C	Peat A1	Heath Bald Sand A2	Transi- tion B	Spruce- fir C
8-7-28							
6- 6:30 A. M. ....	49F	49F	49F	56F	52F	54F	53F
8- 8:20 .....	55	52.5	51	56	59	54	53
10-10:25 .....	62.5	60	57.5	57	71	55	53
12-12:15 .....	67.5	62	61	57	74	57	54
1:45-2:05 .....	69	61	62	59	83	57	56
4- 4:10 .....	61	59	57	60	74	57	55
7- 7:15 .....	52	52	53.5	59	62	56	54
8-9-30							
7:15 A. M. ....	65F	---	61F	60F	---	---	53F
8:35 .....	72.5	---	67	61	---	---	54
9:45 .....	75	---	67	60	---	---	54
10:40 .....	77	---	69.5	61.5	---	---	54.5
12:50 .....	96	---	75	65	---	---	55
2:30 .....	93	---	75	70	---	---	55
3:20 .....	82.5	---	71	68	---	---	55
4:20 .....	74	---	66	68	---	---	55
5:00 .....	69	---	66	67	---	---	55

by heath balds, as in the tributary region of Roaring Fork, west of Brushy mountain, that one expects to find the answer to their distribution therein. It is not so simple a matter, however, as increased xerophytism of habitat due to southern exposure. The problem is further complicated by balds occurring elsewhere on all exposures, north, east and west, as well as south. Neither is the angle of slope a determining factor. On certain precipitous ridges, as the Chimney Caps, one would readily believe that trees can not hold on; and that may be partly true, but many slopes far exceeding 45 degrees in steepness are heavily forested, as in the Trout Creek and Alumn Cave region, while gentler slopes on Brushy mountain are bald. The relation of the slope and the heath bald position seems to be one of direction of prevailing winds. In a broad sense, the prevailing winds are from the southwest, but in the mountains they are variously deflected and the heath balds seem always to be on the windward side, a position of importance during the severe winter weather.

Certain characteristics of the soils of the heath balds, notably hydrogen-ion concentration and attendant factors, as peat formation, are considered elsewhere by the writer, Cain (2), but the matter of podsolization of the soil deserves special attention.

A podsolized soil is one with a gray leached layer in the profile which,

strictly speaking, is termed the "podsol," from the Russian "sola," meaning ash. Recently, however, the term has been applied, not only to the leached layer, but to the whole soil profile and even to the process of development. There are essentially three regions which make up the podsol profile: (1) a raw humus layer on top, beneath which is, (2) the gray leached podsol region, and underneath this, (3) a brown enriched layer. Podsolization occurs to a certain extent in the soils of the hemlock, pine-heath and birch woods, but is especially characteristic of the soils of the spruce-fir and the heath bald regions.

The best development of the podsol type observed by the writer in the Great Smoky mountains is on the Brushy mountain heath bald, Table XIV. Figure 3 presents a photograph of one typical profile from Brushy mountain at an elevation of almost 5,000 feet. In this profile we are able to distinguish more than three layers. On the surface is a thin layer of dry peat (A 1) (Table XIV) which has been designated as "trochentorf" and has a wide distribution in heath balds at lower altitudes and in pine heath. Beneath this is found a considerable quantity of moist brown peat (A 2) in which the vegetative structure is well preserved. This layer gradually darkens downward into the brownish-black soil humus-layer (A 3). These first three layers of the organic horizon are extremely acid and provide the dissolving substances so important in the formation of the ash gray leached layer (A 4), the "podsol" layer. Beneath the A horizon is the enriched B horizon, ochre-yellow to deep brown in color. An unusually compact "ortsstein" layer is found at the top of the B horizon (B 1). This hardpan is a solidification of substances carried down by the percolation of dissolving substances from above and precipitated at the bottom of the leached zone (A 4). This particular ortsstein can be lifted out of the soil in large layers from  $\frac{1}{8}$  to  $\frac{3}{8}$  of an inch in thickness, so solid that they resemble iron concretions. Beneath the ortsstein is a layer (B 2) also enriched but uncemented and effectively cut off from the roots of the plants above by the iron pan. Lower down is the C horizon of "Muttergestein," or inorganic parent material.

The podsol type of soil development is considered in detail by Hans Jenny (10), who emphasizes the climatic relationships involved in its formation. Christopherson (3), in his studies on soil reaction in Sylene National Park, Norway, also arrives at the conclusion that climatic factors are of primary importance in podsol development, especially



Figure 3. Podsol Profile from Brushy Mountain Heath Bald. The white line in the photograph is a string placed on the transition line from the peat layer to the gray-leached podsol.

TABLE XIV

## PODSOL PROFILE, BRUSHY MOUNTAIN HEATH BALD

Horizon	Zone	Thickness	Name or Description
A.....	1	0.5 cm	Trochentorf
	2	8.0 cm	Brown fibrous peat
	3	2.0 cm	Black humus transition
	4	13.0 cm	Gray-leached podsol
B.....	1	0.5 cm	Ortsstein, iron hardpan
	2	15.0 cm	Enriched brown Zone
C.....	1	10.0 cm plus	Subsoil

precipitation and temperature. He says: "In a general way, a low average temperature with a high average precipitation are favorable for podsol development." Three recent papers on work done in eastern United States emphasize the importance of podsolization in silviculture, Fisher (7), Lutz (14) and Stickel (19). They confirm the importance of abundant rainfall and cool temperatures, especially severe winters, but add that podsol soils can also develop in regions with more favorable climate as a result of producing pure stands of timber, especially conifers. It is desirable to emphasize the wide development of the podsol type in associations dominated by broad-leaved evergreen species, as the Ericaceæ of these balds. The development of the podsol and Ortsstein layers the writer believes to be particularly important in the heath bald associations, since the vegetative habits of the heath bald species fit them for existence in the podsolized soil. Their root systems are shallow and the plants spread horizontally by rhizomes. The result is a dense mat of interlocking roots in the A horizon of the soil, with few if any penetrating the Ortsstein layer.

**CATASTROPHIC FACTORS.**—There seem to be three catastrophic factors influencing the formation and maintenance of heath balds in the Great Smoky mountains; they are windfall, landslide and fire. Of these factors, fire is by far the most important.

The effect of repeated fires can be seen on Brushy mountain. The last three fires have burned successively smaller areas. Passing into the treeless area from Beech Gap, sometimes known as Grassy Gap, the trail goes under a thicket of Rhododendrons, Kalmia and other heath bald species eight to ten feet high, growing so dense that it is impossible to leave what was until recently only a bear trail except by cutting away the brush. In the area of the second burn the shrubs are four to five



gnarled balls of root stocks and old stem bases a foot or two in diameter which have withstood many fires and the destruction of aerial parts. Other species less characteristic of the balds, as *Acer rubrum*, *Prunus pennsylvanicum*, *Betula lenta* and *B. lutea*, frequently make a scattered appearance after fires, enjoy a rather enfeebled growth and succumb during the next conflagration if not before. The ericads are so resistant to fire and sprout back so readily that other species characteristic of the contiguous forests have little chance of permanent invasion into bald areas subject to repeated fires.

Many mountaineers and woodsmen familiar with the region, as Mr. Andy Gregory, of the Little River Lumber Company, and Mr. Horace Kephart, of Bryson City, North Carolina, who are unusually close observers, think that fire is a very important if not universal factor in the initiation and maintenance of heath balds. Mr. Gregory recently told the writer that he has dug through one or two feet of peat in heath bald areas where there is no present indication of there having been a fire, but inevitably there is a charcoal layer at the bottom of the peat. The writer has had the same experience in many places. In some instances a black humus layer could be mistaken for charcoal, but even in a *Betula lenta* consociation at about 4,300 feet on the north side of Mt. LeConte I have found charred wood beneath a few inches of fibrous brown peat. Davis (5), working in the Black mountains of North Carolina, came to the conclusion that fire is an extremely important factor in this connection.

Despite the frequent importance of fire in eliminating trees from potential heath bald areas, it is not an exclusive factor, especially at higher altitudes, where landslides and windfalls are important contributing factors. Landslides have been conspicuous during the last two or three years in the vicinity of Dry Sluice Gap on the state line, on the Little Pigeon side of the Sugarland mountain near the Chimneys and on the upper Roaring Fork side of Mt. LeConte. It will be instructive to observe the return of trees or the establishment of balds in certain parts of these areas, as the case may be. Windfalls are numerous in the shallow-rooted spruce forests and especially where the fir, *Abies fraseri*, is dominant at higher elevations. When windfalls occur in locations suitable for the maintenance of heath balds, it is believed by the writer that trees do not come back.

In many situations, as along the divide between Myrtle Point,

LeConte and the state line, and in certain places along the trail above Alum Cave, *Rhododendron catawbiense*, *R. punctatum*, etc., are so well-developed that they almost form a continuous cover under the spruce and fir. One can easily see that the elimination of trees by windfall or landslide would permit the closing in of the Rhododendrons and the establishment of heath balds. Soil and air conditions favoring the germination and establishment of conifer seedlings would be largely destroyed by the elimination of the tree cover, but the heath bald species could sprout and vegetate, rapidly forming a closed cover.

In brief summary of this section, it seems to the writer that the heath balds, from a successional point of view, are definitely postclimax, Weaver (24). Heath bald species occur under the protection of the contiguous forest, and in more favorable locations (that is, more favorable for the heath bald species) they are so abundant that it seems clear that the elimination of the trees by catastrophic forces would result in establishment of balds, which would effectively, in many instances, prevent reinvasion by the forests.

## SUMMARY

1. The ecology of a type of vegetation in the United States, apparently peculiar to the Southern Appalachian mountains and especially the Great Smoky mountains, is considered from a number of angles. These plant communities, here described for the first time, are referred to as "heath balds" because of their two most apparent aspects: (a) the dominant shrub flora is largely composed of species belonging to the heath family, Ericaceæ and (b) trees are absent from well-developed examples of this association.

2. The heath balds occur as restricted areas mainly on the windward sides of upper slopes and peaks with an altitudinal range of approximately 4,000 to 6,500 feet, being more frequent in the subalpine zone.

3. The heath balds have a fairly constant physiognomy throughout this altitudinal range, despite a considerable change in species content, and can be described briefly as broad-sclerophyll scrub with a considerable content of evergreen species. These facts are brought out by tables of the following data: (a) the relation of the flora of these island-like areas to the contiguous forests, (b) the change in species content with change in altitude, (c) an analysis of the flora according to Raunkiaer's

life-form classes and (d) leaf-size classes. Further statistical information on frequency and dominance is gained by use of quadrats on Brushy mountain.

4. The problem of the initiation, maintenance and distribution of the heath balds is considered on a basis of climatic, edaphic and catastrophic factors. It is concluded that the heath balds are postclimax, and consequently are derived from the contiguous forest associations as the result of the interaction of a number of factors. The combination and intensity of these factors may be various in the production of different heath balds by the local deterioration or destruction of the forest.

5. With cool and humid climatic conditions and evergreen vegetation, there is a decided development of edaphic conditions, as high acidity, peat formation and podsolization, which progressively favor heath bald species. In many places it is apparent that the elimination of the trees would permit the undershrubs to develop a closed cover, which they are apparently quite capable of maintaining, in most instances, against the encroachment of trees.

6. The biological equipment of the ericads is such as to favor them in competition with other plants under these rather extreme edaphic and climatic conditions, yet it must be understood that their occupancy of these areas is due more to their tolerance of the conditions, since their vitality is greater under the protection of trees.

The writer wishes to express gratitude to Professor George D. Fuller, of the University of Chicago, for suggesting the possibilities for ecological research in the Great Smoky mountains, and who has constantly guided these efforts during the past four years.

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